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Studies on the Deep Sea Protobranchia: The Subfamily Ledellinae (Nuculanidae)

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CONTENTS

Synopsis Fourteen species of *Ledella* occurring in the Atlantic are described, five of which are new species, namely, *L. jamesi*, *L. lusitanensis*, *L. sandersi*, *L. similis* and *L. verdiensis*.

Species of the subfamily Ledellinae are usually small, less than 7 mm total length, with shells that are solid, concentrically ridged, ovate, medially or submedially rostrate, and with an amphidetic predominantly internal ligament.

The morphology of *Ledella* is very conservative, the only organ that shows any marked variation in form is the hind gut. Five different configurations of the hindgut occur and these can be derived by radiate or sequential evolution from the primitive condition in which the hind gut forms a single deep loop on the right side of the body.

Although the three most widely distributed species are confined to abyssal depths, endemic species also occur at abyssal depths in individual basins.

The most common species, *L.ultima*, is distributed throughout the Atlantic over a wide depth range. Its success can not only be related to the possesion of a greatly extended hindgut, and therefore a more efficient digestive ability, but also to the fact that the oldest specimens show a marked change in the direction in the growth of the shell edge. The effect of this latter is to increase the shell space and providing more for eggs in comparison to those species that do not have this peculiarity of growth. Egg and prodissoconch size indicate that development is lecithotrophic with a short distributional larval phase.

INTRODUCTION

This is the sixth paper in a continuing series devoted to the taxonomy, ecology, functional morphology of the Protobranchia of the deep Atlantic (Allen & Sanders, 1973, 1982; Sanders & Allen, 1973, 1977, 1985).

In this paper we turn to the genus *Ledella* Verrill & Bush, 1897. Here we consider fourteen species and four subspecies. Eight of the species have been previously described. These latter descriptions are mostly concerned with shell features, many of them are inaccurate and incomplete with no, or at most, scanty, detail of the internal morphology. The subfamily Ledellinae was defined in an earlier paper in the series (Allen & Sanders, 1982) and compared with the Spinulinae and this description is also given in an account of the taxonomy of the protobranch bivalves of the world (Allen & Hannah, 1986) and need not be repeated here other than to state that it is a predominantly abyssal group of small, characteristically rostrate, shells, in which the rostrum is medial or submedial and the ligament is internal or predominantly so. Although additional genera have been described recently from the Pacific (Filotova & Schileko, 1984), in the Atlantic two genera are recognised, namely *Ledella* (see Warén, 1981) and *Tindariopsis*.

The subfamily is of considerable interest in that within it is exhibited almost the full range of hind gut configurations that occur in the subclass Protobranchia, and thus illustrate the evolutionary pathways by which these configurations have been achieved. The subfamily also contains one of the most common species of protobranch molluscs present in deep water (*L. ultima*), with samples sufficiently large to form some opinion as to its ecology and the reasons for its success. Finally, from the wealth of material at our disposal, this study is able to correct a number of taxonomic discrepancies that have appeared in the past literature.

We would like to thank the following people for their interest, support, discussion and their contribution of material and for many other kindnesses without which this contribution would have been much the poorer.

Dr. H. L. Sanders and Dr. F. Grassle, Woods Hole Oceanographic Institution; Dr. A. Warén, Swedish Museum of National History, Stockholm; Dr. Jorgen Knudsen, University of Copenhagen; M. P. Bouchet, Museum National d'Histoire Naturelle, Paris; M. Segonzac, Centob, Brest; Dr. J. Taylor and the staff of the Mollusca Section of the British Museum of Natural History. As in the previous papers in this series, we describe one common species in considerable detail and use this description as a basis for comparison with other species and, in descriptions of the latter, only list features that define and differ from those first described.

Abbreviations to text figures

aa: anterior adductor
ag: gland aperture
an: anus
apr: anterior pedal retractor muscle
as: anterior sense organ
by: byssal gland
cg: cerebral ganglion
cn: central nerve
co: viscero-cerebral commissure
dh: dorsal hood
di: digestive diverticula
fa: feeding aperture
fr: faecal rod
ft: foot
gc: gland cells
gi: gill
gs: gastric shield
hg: hind gut
ht: heart
if: inner mantle fold
ky: kidney
li: ligament
ma: mantle
mf: muscle fibres
mfs: middle mantle fold
mh: mouth
ni: nuclei
oe: oesophagus
of: outer mantle fold
ov: ovary
pa: posterior adductor
pb: palp proboscis
pe: periostracum
pg: pedal ganglia
pp: palp
ppr: posterior pedal retractor muscle
rj: rejection tract
sa: divided sole of foot
sf: secondary mantle fold
si: siphon
sr: sorting ridges
ss: style sac
st: stomach
sy: statocyst
te: tentacle
tm: transverse muscle
ts: testis
vg: visceral ganglion

Family **NUCULANIDAE** Adams & Adams 1858

Subfamily ***LEDELLINAE*** Allen & Sanders 1982

Shell robust, elongate, moderately inflated, veneriform or ovate with characteristically short rostrum, rostrum medial or submedial, concentric sculpture, usually marked but occasionally faint, in some species incomplete radial striae present; umbo approximately central; posterior dorsal margin convex, ventral margin of older specimens characteristically broad and flat, postero-ventral margin sinuous to a greater or lesser degree; hinge plate well developed, hinge teeth stout chevron-shaped; ligament internal and/or external; hindgut with various configurations; adductor muscles approximately equal in size; siphons combined, but usually form a single lumen, palps with relatively few ridges.

Ledella Verrill & Bush 1897

Type species. *Leda ultima* Smith 1885; by subsequent designation.

[*nom. sub. pro Ledella messanensis* (Seguenza MS); Verrill & Bush, 1897, (non Seguenza MS *in* Jeffreys, 1870) = *Ledella bushae* Warén, 1978 (ICZN, 1985. Opinion 1306); herein, (ICZN 1985. Art. 78 F (iv).]

Type locality. Challenger Sta. 5, 24° 28′W, 5011 m. southwest of the Canary Islands.

Synonomy. *Junonia* Seguenza, 1877 (non Hübuer, 1818); *Comitileda*, Iredale, 1924; *Magaleda*, Iredale, 1919.

Shell small, short, robust, surface matt, concentric sculpture with scattered incomplete, radial striae in some species, well defined rostrum, usually unicarinate at margin of escutcheon; ventral margin broadly flattened in older specimens of some species, postero-ventral margin sinuous; anterior and posterior hinge teeth series separated by amphidetic, internal ligament, central apex of outer layer of ligament visible externally; hind gut loops in various configurations.

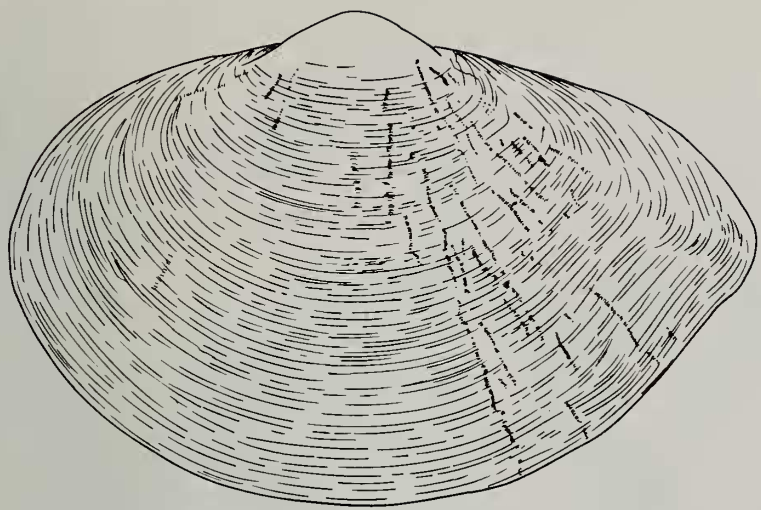

Fig. 1 *Ledella pustulosa pustulosa*: Shell drawn to show lateral view of left valve of a specimen from Biscay. (Sta. Biogas I, DS11). (Scale = 1 mm).

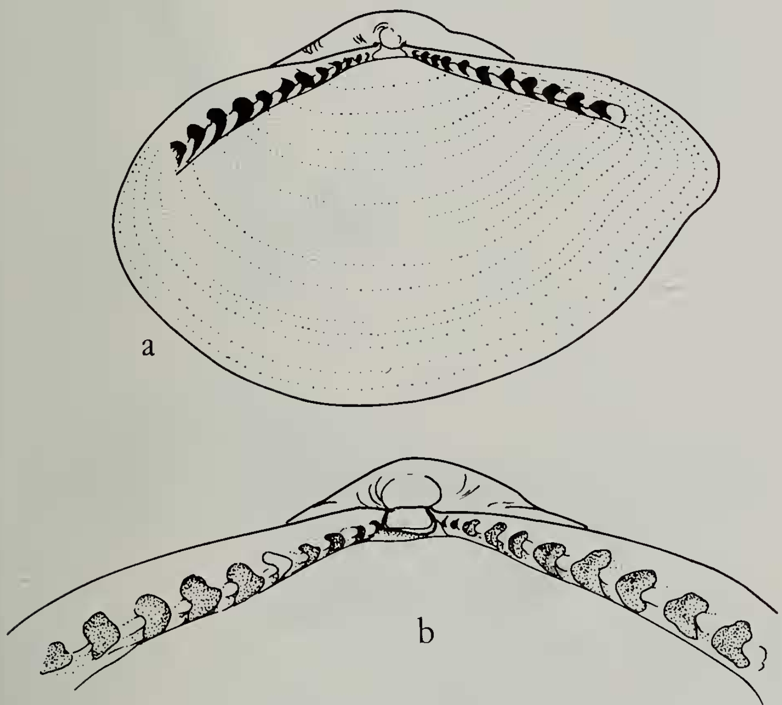

Fig. 2 *L. pustulosa pustulosa*: a) Internal view of right valve of a specimen from Biscay. (Sta. Biogas IV. CP01); b) Detail of hinge plate of left valve of the lectotype (BMNH No. 85.11.5.482). (Scale = 1 mm).

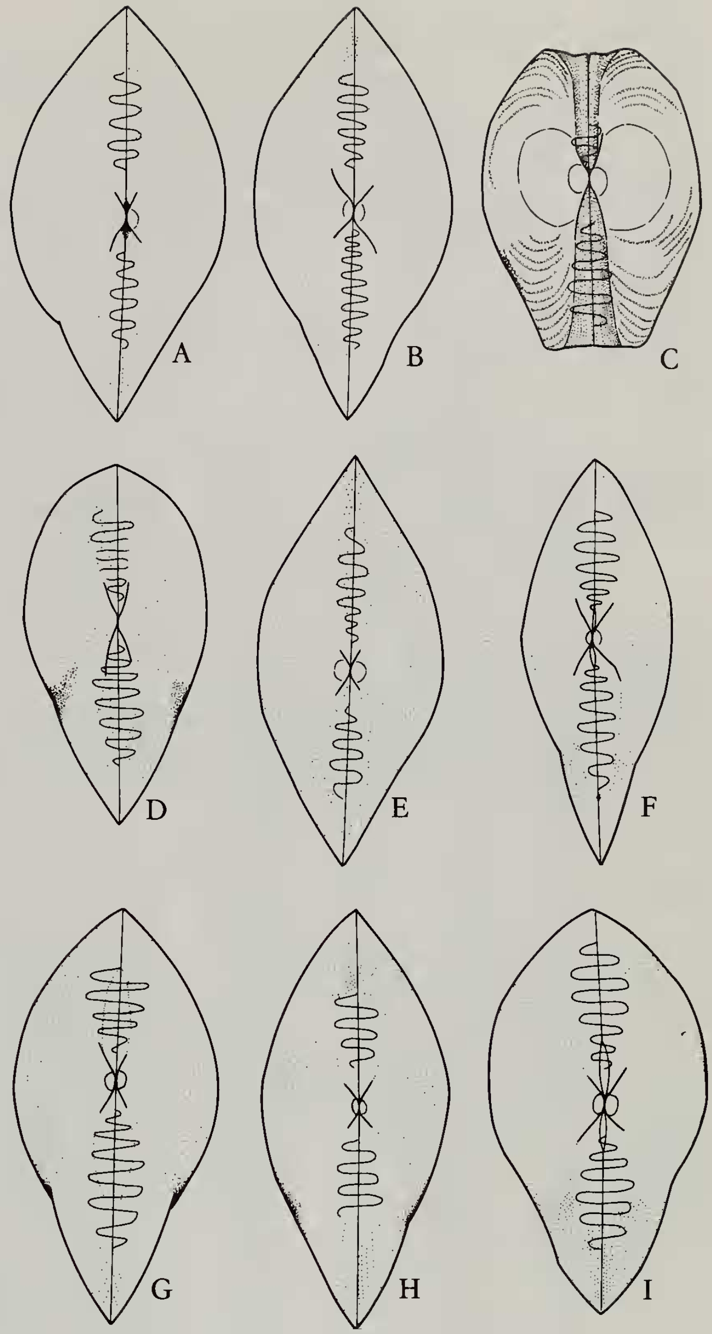

Fig. 3 Dorsal views of the shells of various species of *Ledella* for comparison. *A, Ledella pustulosa marshalli*; B, *L. pustulosa pustulosa*; C, *L. ultima*; D, *L. lustanensis*; E, *L. pustulosa argentinae*; F, *L. acuminata*; G, *L. sublevis*; H, *L. jamesi*; I, *L. solidula*.

Ledella pustulosa pustulosa (Jeffreys, 1876)

LECTOTYPE. British Museum (Natural History) BM(NH) 18 85.11.5.482.

TYPE LOCALITY. Porcupine Expedition (1869) Station 23a, West of Ireland, 768 m.

Because at least six species are included in the previously identified collections of this species that are present in the U.S. National Museum (USNM) (see below) we have assigned a lectotype from the material present in the British Museum of Natural History (BMNH). From an extensive synonymy only those listed below can be ascribed to *L.p. pustulosa* with certainty.

SYNONYMY. *Leda pustulosa* Jeffreys, 1876. *Ann. Mag. Nat. Hist.* Ser. 4, *18*, p. 430 (in part).
Leda (Junonia) pustulosa Jeffreys: Seguenza, 1877. *Atti Reale Accad. Lincei Mem.* Ser. 3, *1*, p. 1177, pl. 3, fig. 17.
Leda pustulosa Jeffreys: Jeffreys, 1879. *Proc. Zool. Soc. Lond.* 1879. p. 576 (in part).
Nuculana pustulosa (Jeffreys): Smith, 1889. *Ann. Mag. Nat. Hist.* Ser. 4, *6*, p. 425.
Leda pustulosa Jeffreys: Locard, 1898. *Exp. Sci. Traveilleur Talisman*. p. 345.
Leda pustulosa Jeffreys: Friele & Grieg, 1901. *Norw. N. Atl. Exped. 6*, p. 28.

MATERIAL. The following specimens labelled *L. pustulosa* in the collections of the USNM & BMNH were examined.
USNM No. 199581 Porcupine 1869 st. 16, 1492 m in part (2 other species present)
USNM No. 199575 Porcupine 1869 st. 23, 1214 m
USNM No. 199576 Porcupine 1869 st. 28, 2222 m.
BM(NH) No. 1885.11.5.387–9 Porcupine 1869 st. 28, 2222 m.

USNM No. 199579 Porcupine 1869 st. 58, 987 m.
USNM No. 199580 Porcupine 1869 st. 2, 557 m.
USNM No. 199586 Travailleur st. 3,1262m. ?(Museum label does not match station list on Locard text)
USNM No. 199582 Porcupine 1870 st. 17a, 1353 m*
USNM No. 199583 Porcupine 1870 st. 17a, 1353 m.*
USNM No. 199584 ? Origin, in part (1 other species present)
**L. p.hampsoni* (see p. 138)

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			WEST EUROPEAN BASIN				
La Perle	DS06	2090	2	47°30.5′N	8°18.5′W	DS	6. 8.72
(Biogas I)	DS07	2170	5	47°30.5′N	8°15.5′W	DS	6. 8.72
	DS09	2130	4	47°30.2′N	8°16.0′W	DS	7. 8.72
	DS11	2205	11	47°35.5′N	8°33.7′W	DS	8. 8.72
	DS12	2180	4	47°28.5′N	8°35.5′W	DS	9. 8.72
	DS13	2165	12	47°33.7′N	8°39.9′W	DS	9. 8.72
Jean Charcot	DS32	2138	56	47°32.2′N	8°05.3′W	DS	19. 4.73
(Biogas II)							
(Biogas III)	DS35	2226	8	47°34.4′N	8°40.7′W	DS	24. 8.73
	DS36	2147	7+2V	47°32.7′N	8°36.5′W	DS	24. 8.73
	DS37	2110	19	47°31.8′N	8°34.6′W	DS	24. 8.73
	DS38	2138	26	47°32.5′N	8°35.8′W	DS	25. 8.73
	DS49	1845	13	44°05.9′N	4°15.6′W	DS	1. 9.73
	DS50	2124	15+1V	44°08.9′N	4°15.9′W	DS	1. 9.73
(Biogas IV)	DS51	2430	3+1V	44°11.3′N	4°15.4′W	DS	18. 2.74
	DS52	2006	47	44°06.3′N	4°22.4′W	DS	18. 2.74
	DS62	2175	18	47°32.8′N	8°40.0′W	DS	26. 2.74
	DS63	2126	78	47°32.8′N	8°35.0′W	DS	26. 2.74
	DS64	2156	58	47°29.2′N	3°30.7′W	DS	26. 2.74
	CP01	2245	21	47°34.6′N	8°38.8′W	CP	25. 2.74
	CP02	2177	2	47°33.2′N	8°41.4′W	CP	26. 2.74
	KR39	2179	2	47°33.8′N	8°36.4′W	KR	25. 2.74
Cyros	DS70	2150	1	44°08.8′N	4°17.4′W	DS	21. 6.74
(Biogas V)	CP07	2170	28	44°09.8′N	4°16.4′W	CP	21. 6.74
Jean Charcot	DS71	2194	44	47°34.3′N	8°33.8′W	DS	20.10.74
(Biogas VI)	DS86	1950	76	44°04.8′N	4°18.7′W	DS	31.10.74
	DS87	1913	123	44°05.2′N	4°19.4′W	DS	1.11.74
	DS88	1894	7	44°05.2′N	4°15.7′W	DS	1.11.74
	CP08	2177	16+3V	44°33.2′N	8°38.5′W	CP	20.10.74
	CP09	2171	14+1V	47°33.0′N	8°44.1′W	CP	20.10.74
	CP24	1995	9+5V	44°08.1′N	4°16.2′W	CP	31.10.74
	CP25	1894	6+2V	44°05.0′N	4°17.0′W	CP	1.11.74
Jean Charcot	DS15	2246	4	47°35.2′N	8°40.1′W	DS	21.10.72
(Polygas)	DS18	2138	8	47°32.2′N	8°44.9′W	DS	22.10.72
	DS25	2096	16	44°08.2′N	4°15.7′W	DS	1.11.72
	DS26	2076	57+1V	44°08.2′N	4°15.0′W	DS	1.11.72
	CV10	2108	5	47°30.7′N	8°40.6′W	CV	22.10.72
Thalassa	Z453	1975–2070	5	48°34.0′N	10°51.6′W	CP	28.10.75
Sarsia	44	1739	1	43°40.8′N	3°35.2′W	ED	16. 7.67
	65	1922	31	46°15.0′N	4°50.0′W	ED	25. 7.67
Jean Charcot	DS01	2091	1246	57°59.2′N	10°41.3′W	DS	15. 7.76
(Incal)	KR01	2093	1	57°59.2′N	10°41.3′W	KR	16. 7.76
	DS02	2081	2135	57°58.5′N	10°49.2′W	DS	16. 7.76
	CP01	2068–2040	408	57°56.4′N	10°55.0′W	CP	16. 7.76
	CP02	2091	27	57°57.7′N	10°44.6′W	CP	16. 7.76
	DS03	609–619	3	57°24.8′N	11°04.0′W	DS	17. 7.76
	DS05	2503	3	56°27.6′N	11°12.0′W	DS	18. 7.76
	CP08	2644	1	50°15.2′N	13°14.8′W	CP	17. 7.76
	CP09	2659	2	50°14.3′N	13°16.1′W	CP	27. 7.76
	OS01	2634	1	50°15.2′N	13°11.0′W	OS	30. 7.76
	WS01	2550–2539	4	50°19.3′N	13°06.9′W	WS	30. 7.76
	WS02	2498–2505	25	50°20.0′N	12°56.0′W	WS	30. 7.76
Chain 106	313	1500–1491	456	51°32.2′N	12°35.9′W	ES	17. 8.72
	314	1006–1015	1	51°54.7′N	12°27.3′W	ES	18. 8.72
				–50°58.7′N	13°01.6′W		
	316	2173–2209	12	50°57.7′N	13°01.3′W	ES	18. 8.72
	318	2506	6	50°27.3′N	13°20.9′W	ES	19. 8.72
				–50°26.8′N	13°19.9′W		

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			CANARIES BASIN				
Discovery	6701	1934	43	27°45.2′N	14°13.0′W	ED	16. 3.68
	6704	2129	6	27°44.9′N	14°25.0′W	ED	17. 3.68

This is one of four closely related subspecies described here.

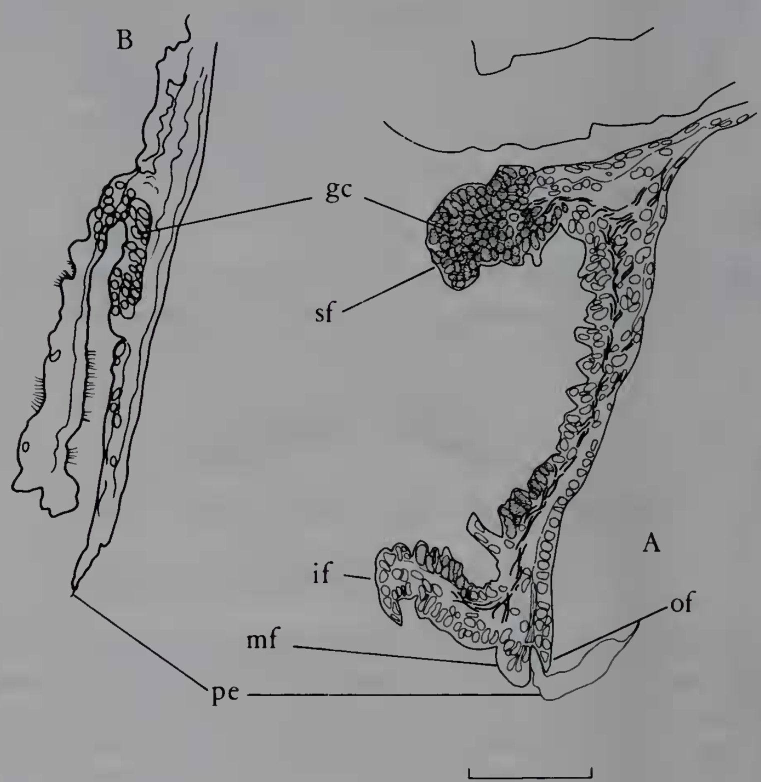

Fig. 4 *L. pustulosa pustulosa*: (A) Transverse section of mantle edge through region of posterior feeding aperture; (B) Transverse section through the anterior sense organ of the mantle. (Scale = 0.05 mm).

DESCRIPTION (Figs 1, 2, & 3). Shell ovate, rostrate, moderately thin, often somewhat transparent, moderately inflated; periostracum straw coloured, preserved specimens may appear 'blistered' giving a tortoise-shell effect, slightly iridescent; sculpture, fine concentric ridges, distance between ridges variable, ridges intersected by radial striae from umbo to ventral margin; radial markings vary from faint to conspicuous, may be obvious across whole shell but usually most obvious around umbo and close to sinuosity, in some striae only observed with difficulty; dorsal margin weakly convex, antero-dorsal margin gradually inclined to anterior limit of hinge plate, then slopes rapidly to form curve of anterior margin, postero-dorsal margin gradually slopes to posterior limit of hinge plate, then forms posterior dorsal margin of short rostrum, posterior ventral margin sinuous, ventral margin long, moderately convex, smoothly curved; umbo approximately equilateral or very slightly displaced posteriorly (average umbo to posterior margin length/total length = 0.48), umbo moderately inflated and posteriorly directed, keel extends from umbo to tip of rostrum, concentric ridges form acute angle at keel; hinge plate moderately strong, long, fairly narrow, 6–12 anterior and posterior chevron-shaped teeth (number depending on size), distal teeth strong, proximal teeth becoming progressively smaller, innermost difficult

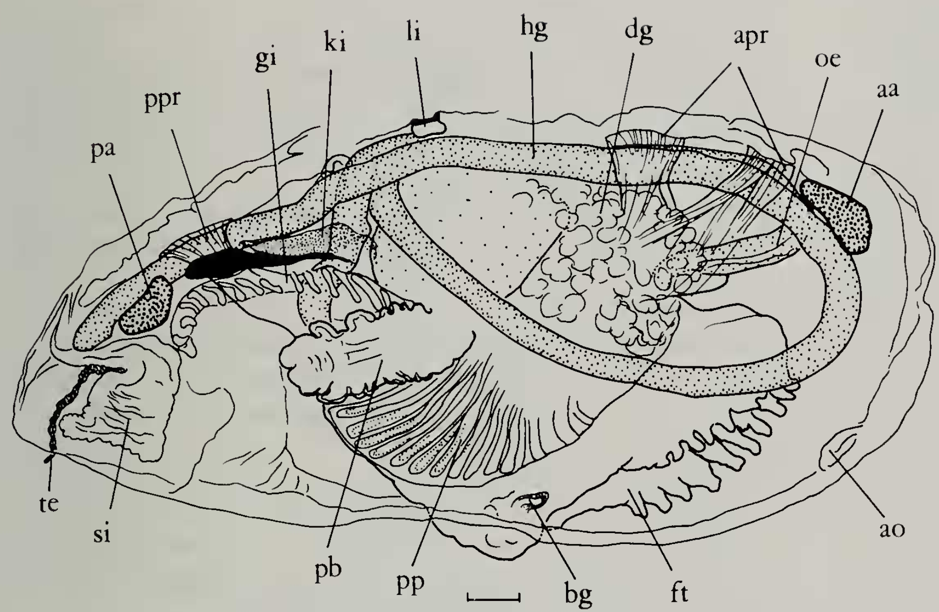

Fig. 5 *L. pustulosa pustulosa*: Lateral view of specimen from right side with shell removed to show the arrangement of the body organs. Note only the section of hind gut to the right side of the body is shown. (Scale = 0.1 mm).

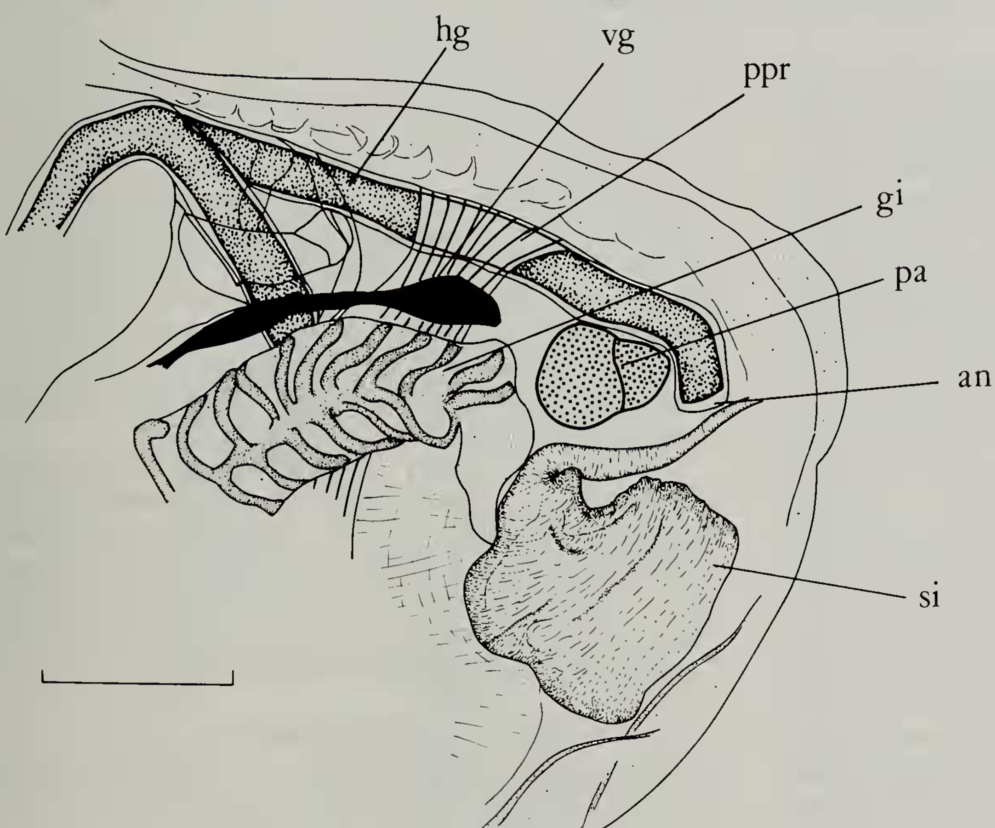

Fig. 6 *L. pustulosa pustulosa*: Detail from lateral view from left side to show detail of siphon and associated organs. (Scale = 0.1 mm).

to discern; ligament amphidetic, internal; resilium, trapezoidal to triangular in shape, moderately large.

Larval shell length 250µm; maximum recorded length 5.61 mm.

MORPHOLOGY. The mantle margin is for the most part unfused and is of the basic bivalve form with three folds. The middle sensory fold is moderately extended as a flap. The inner muscular fold is not greatly thickened, being little thicker than the general mantle epithelium, but is relatively broad. Few gland cells are present in the mantle margin. Posteriorly the mantle forms a siphon combining inhalent and exhalent parts. The combined siphon is a laterally compressed tube, which in preserved specimens, is completely retracted in an S-shape within the shell (Figs. 5 & 6). It is probable that the siphon is extended from a position just below the ventral edge of the rostrum. The siphon is muscular with relatively thick inner and outer epithelial columnar cells.

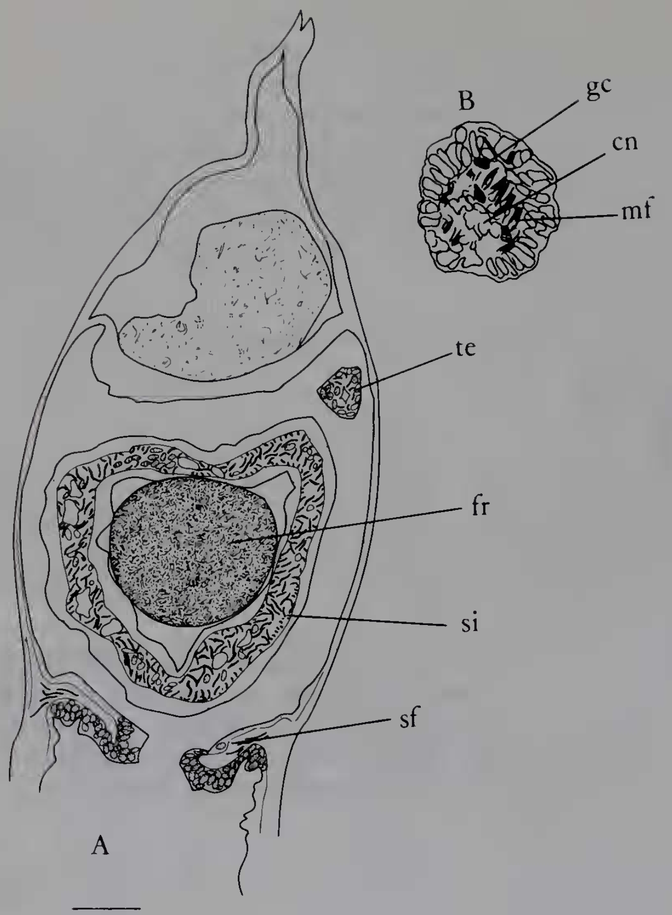

Fig. 7 *L. pustulosa pustulosa*: a) Transverse section through the combined siphon; b) Transverse section through the siphonal tentacle. (Scale = 0.1 mm).

A narrow band of longitudinal muscle fibres lie immediately internal to the basal membrane of the outer epithelium. Internal to the longitudinal layer, the muscles consist of short circular fibres with the occasional transverse fibre between inner and outer basal membranes. Scattered throughout muscle layer are subepithelial gland cells (Fig. 7a). Although considerably contracted and difficult to discern, there is some evidence to suggest that longitudinal muscle blocks are separated by haemocoelic channels. The faecal rod takes up all of the contracted siphonal space (Fig. 7a). We have no evidence of a functional separation formed by a pair of opposing mid-lateral ridges into upper exhalent and a lower inhalent parts as occurs in some protobranchs. The gill axes posteriorly join with the midlateral section of the siphons (Fig. 6) and the posterior gill plates possibly act to channel the faeces into the siphon. The anus lies close to the anterior limit of the siphon.

The siphonal tentacle, derived from the middle sensory fold of the mantle, is a fine thread-like structure that tapers to a point. It originates from a pocket in the right ventral side of the siphonal embayment. In transverse section, it comprises a large central nerve surrounded by fine muscle fibres interspersed with gland cells and connective tissue covered by an outer layer of glandular epithelial cells (Fig. 7b).

A specialized region of the mantle, the feeding aperture, lies ventral to the siphon. Here the inner muscular mantle fold is greatly extended, a secondary fold is also present that forms an arch defining the internal margin of the feeding aperture (Figs. 4a & 7a). A large concentration of acidophilic gland cells are found on this innermost fold, while others are scattered in the epithelium between the two folds and on the dorsal surface of the inner muscular fold proper. The anterior sense organ is a thickened region of the mantle edge directly below the anterior adductor muscle and is similar to that described for *Spinula subexcisa* (Allen & Sanders, 1982). The adductor muscles are approximately equal in size and oval or somewhat crescent-shaped with obvious 'quick' and 'catch' parts.

The gills lie parallel to the posterior dorsal shell margin and are relatively well developed. The number of plates is related to the size of the individual and the maximum number observed in each demibranch was sixteen. The labial palps are moderately large, with 16–23 ridges according to the size of the animal, with large, broad, palp proboscides. The palps extend approximately three quarters across the body; the mouth opens a short distance posterior to the anterior adductor muscle.

The foot is well developed with a relatively narrow neck (Fig. 8b); the divided sole is elongate with a moderately fine papilliate edge. A 'byssal' gland is present, large enough to be obvious as a bulge in the heel of the foot. The gland is spherical and opens medially at the posterior limit of the divided sole (Fig. 8a). The gland is separated from a section of the hind gut above by a layer of transverse muscle fibres. It is encased by peripheral muscles, a few fibres from which possibly form a sphincter at the neck of the gland. The gland itself is composed of large hyaline cells.

The posterior pedal retractor muscles form a thick wide strap which is attached to the shell on either side of the hind gut, just anterior to the posterior adductor muscle. A small postero-lateral pedal retractor muscle is present immediately posterior to the stomach. Three pairs of anterior pedal retractor muscles are attached to the dorsal margin of the shell between the oesophagus and the anterior part of the hind gut. Muscle fibres to the palp proboscides form part of the most anterior of the two sets of anterior muscles (Fig. 5). In section, muscle fibres from the posterior pedal retractor and the innermost anterior pedal retractor cross below the stomach in the neck region of the foot and attach to opposite walls of the foot thus cradling the stomach (Fig. 10b). These muscles may be important in the mixing and movement of the stomach and gut contents. The musculature of the foot itself consists of an outer layer of circular muscles which appear to originate from the posterior pedal retractor and an inner longitudinal layer, anterior in origin.

Conspicuous elongate cerebral and visceral ganglia lie internal to the anterior and posterior adductor muscles repectively. The pedal ganglia are large (Fig. 8b), although not always easily detected in whole mounts, they lie immediately below the most ventral section of the hind gut loop. A large statocyst is associated with each pedal ganglion and lies dorsal to it. The statocyst contains numerous small refractile crystals.

From the mouth the ciliated oesophagus first curves anteriorly to the posterior face of the anterior muscle then follows a course parallel to the dorsal edge of the shell to enter the stomach high on the left anterior face (Fig. 10b). The stomach, with the style sac, takes up a considerable part of the body space. It is dark brown in colour and lies below the resilium. The style sac penetrates approximately half the length of the foot. A large gastric shield occupies more than a third of the stomach wall and is predominately dorsal in position and extends somewhat to the left (Fig. 9). Posteriorly at the junction of style sac and stomach the shield forms a thick chitinous girdle.

That part of the stomach not covered by gastric shield is

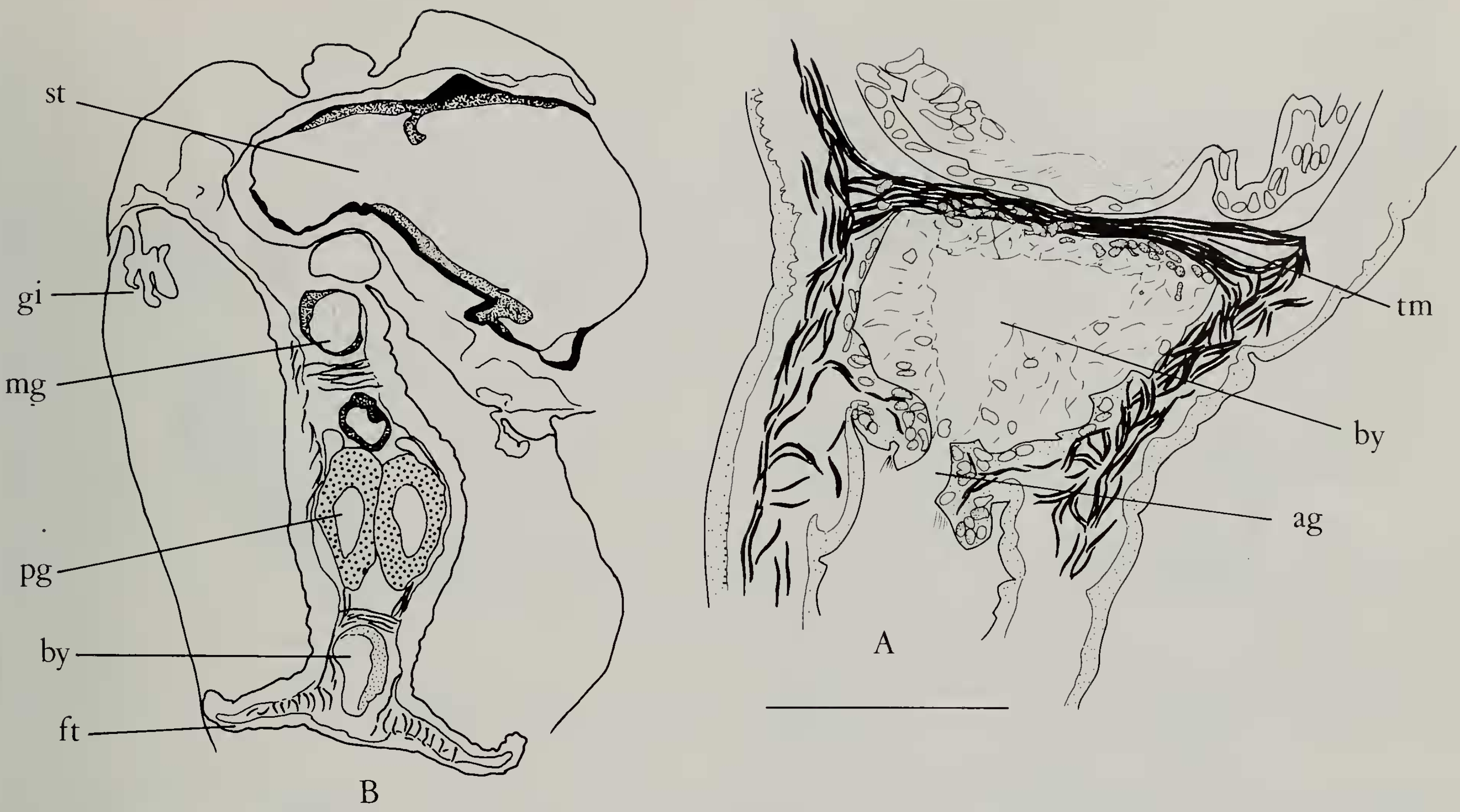

Fig. 8 *L. pustulosa pustulosa*: (a) Vertical transverse section through the 'byssal' gland; (b) Vertical transverse section through the stomach and pedal ganglia. (Scale = 0.1 mm).

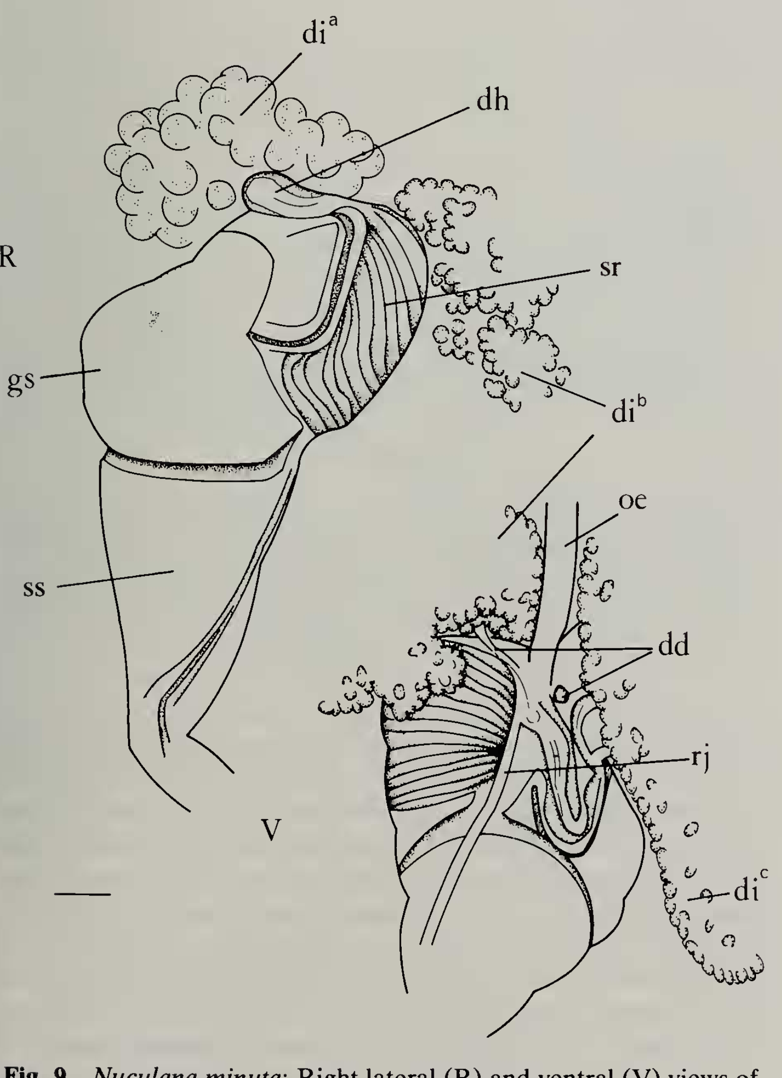

Fig. 9 *Nuculana minuta*: Right lateral (R) and ventral (V) views of the stomach and style sac. (Scale = 0.1 mm).

similar to that described by Yonge (1939) for *Malletia obtusata* and by Purchon (1956) for *Nuculana minuta* (Fig. 9) with the modification that in this deep water species there is a reduction in the number of sorting ridges from fourteen or more to eight. These make up the ciliated portion and form a band of broad ridges, the posterior sorting area that extends across the right side of the stomach (Figs. 9 & 10a) close to the margin of the gastric shield to a line that runs from the lateral margin of the oesophagus, close to an isolated right duct, to the rim of the style sac. At the antero-ventral margin of the posterior sorting area a main rejection tract leads to the midgut. The latter is not separate from the style sac but is guarded from it by major and minor typhlosoles. The major typhlosole extends across the wall of the stomach on the left side to a point below the level of the dorsal hood where it forms a loop close to the apertures of the digestive ducts. It defines a small area referred to by Purchon (1956) as the folded area. It is difficult to be sure in this small species whether this area has transverse folds as those described in *N. minuta*.

The digestive diverticula for the most part cover the anterior wall of the stomach with some posterior extension on either side. They are packed loosely together with little connective tissue between them. One diverticulum lies to the right anterior side and opens to the stomach immediately ventral and to the right of the oesophageal opening. The other two diverticula are situated on the anterior left; one of these opens in the centre of the anterior wall while the other opens more posteriorly and more dorsal to it (Fig. 10a). Externally the appearance of the tubules of this latter diverticulum differ from those of the other two in that their external diameter is larger and that they are paler in colour with a characteristic speckled appearance. The aperture to

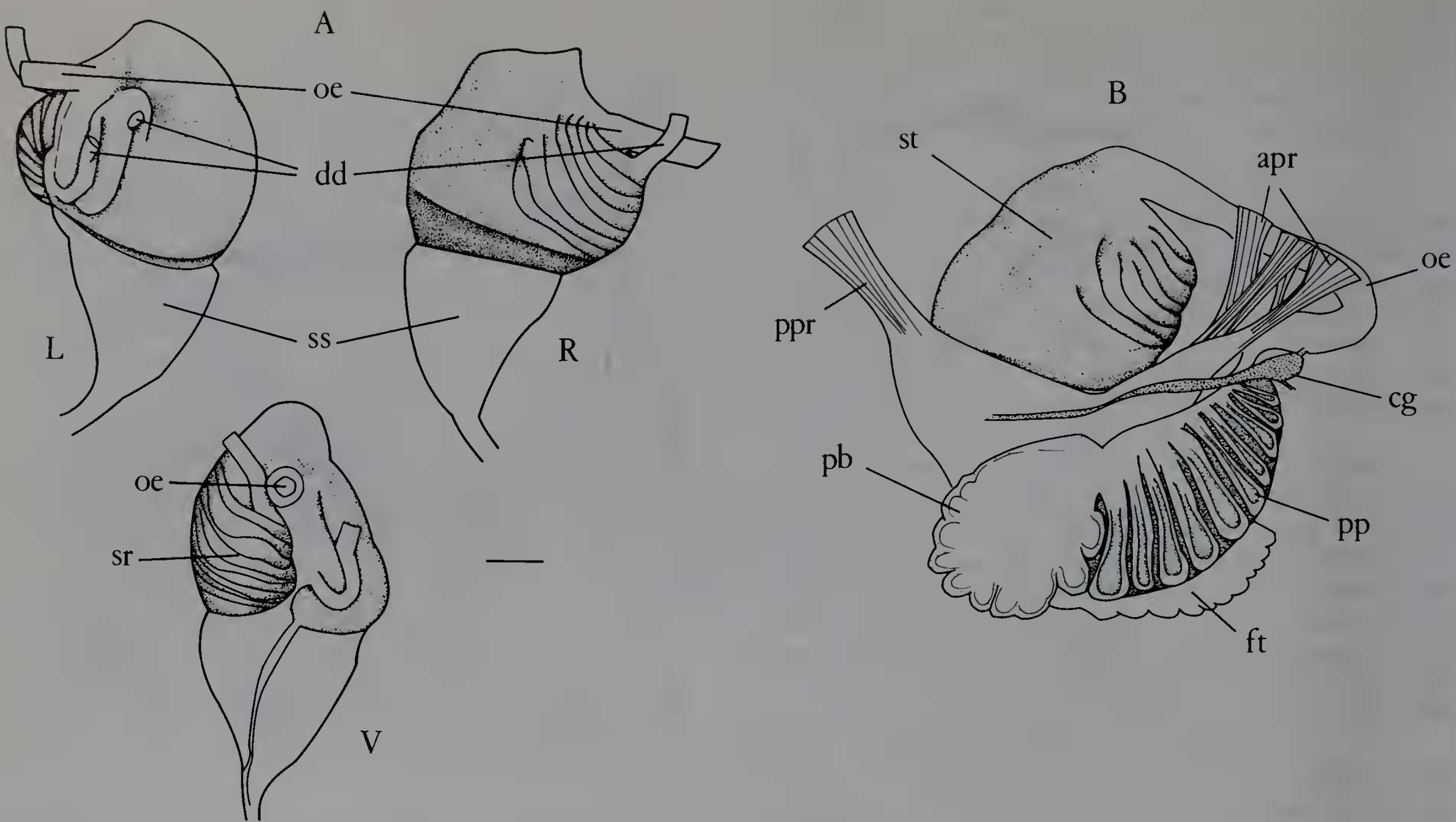

Fig. 10 *L. pustulosa pustulosa*: a) Right (R) left (L) lateral and ventral (V) views of the stomach and style sac, b) lateral view of body, foot and palp from right side. (Scale = 0.1 mm).

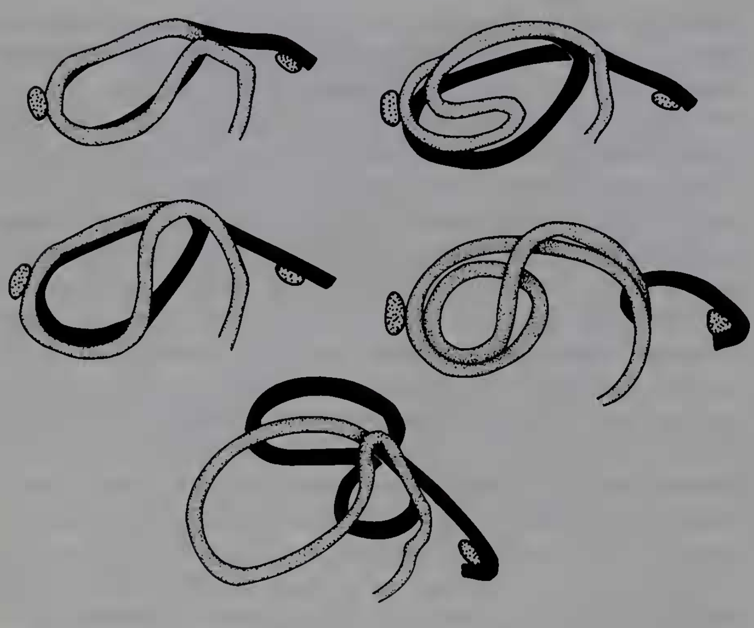

Fig. 11 *L. pustulosa pustulosa*: Variation in the course of the hind gut as seen from the left side. Stippled sections are to the left of the body, black sections to the right of the body. Anterior and posterior adductor muscles are indicated.

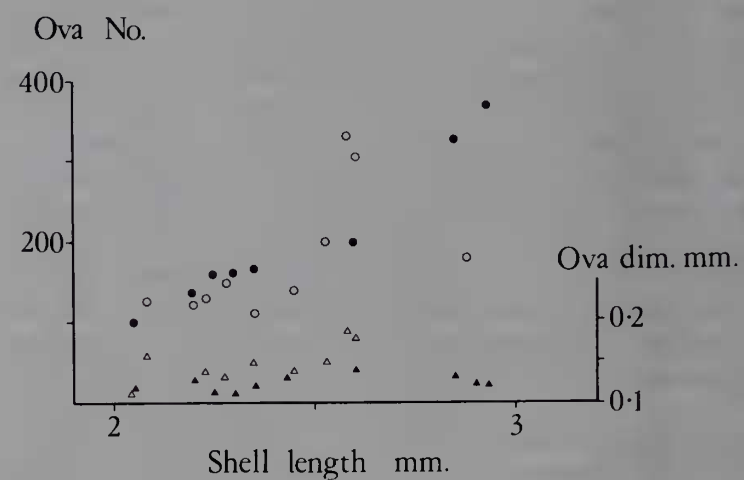

Fig. 12 *L. pustulosa pustulosa*: Ovary development in specimens sampled at different times of the year from similar depths and geographical position. Circles: number of ova; triangles: maximum dimension of ova; open symbols: Biogas III, DS38 (August); closed symbols: Biogas II, DS32 (April).

this posterior dorsal diverticulum opens almost directly to the tubule system, the digestive duct being reduced to a small collar approximately 10 cells deep close to the aperture. Although it appears that the ducts of the other two diverticula are more extended, sections show that what appears to be duct is formed by vacuolated tubule cells. Little material was observed in the lumen of the digestive gland and, when present, it was only in the upper part of the left hand diverticulum.

From the style sac the hind gut extends into the foot first curving anteriorly and ventrally to the pedal ganglion before reversing its course posteriorly and then dorsally behind the stomach. Close to the dorsal margin and immediately posterior to the resilium the hind gut passes to the left side of the body where it forms an anterior loop which curves first ventrally to the anterior adductor muscle and then dorsally and posteriorly to cross to the right of the body anterior to the first crossover point. There it forms a second loop similar to that on the left. Finally, it takes a posterior course close to the dorsal margin passing over the posterior adductor muscle to the anus. An unusual degree of variation in the arrangement of the gut has been observed in this species (Fig. 11). Most of

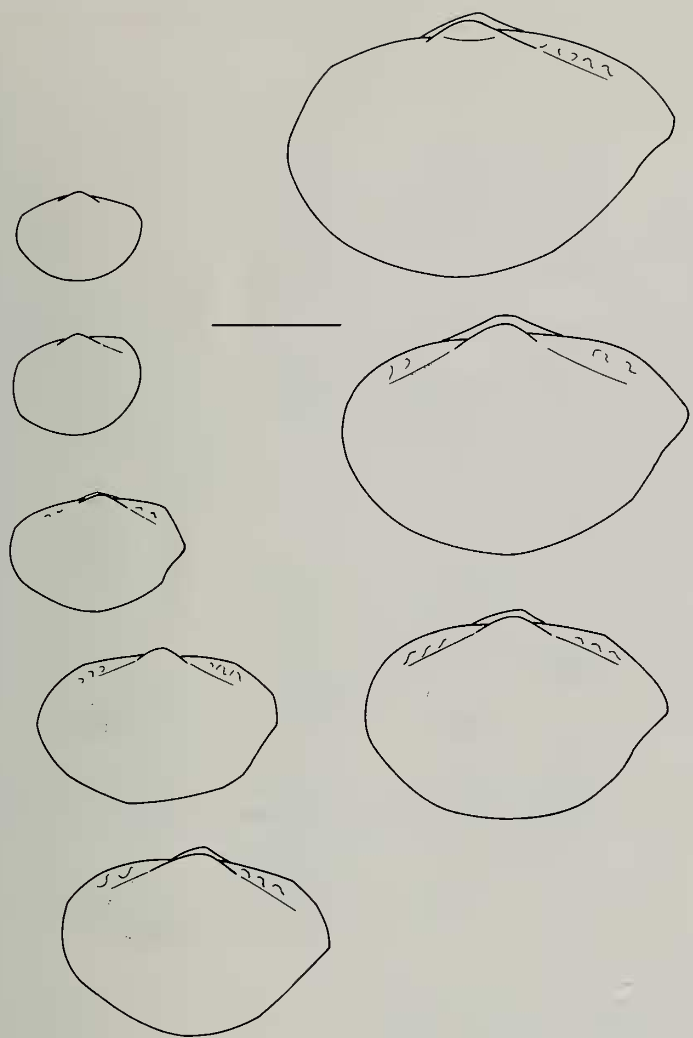

Fig. 13 *L. pustulosa pustulosa*: Growth series of shells in outline seen in right lateral view. (Scale = 1 mm).

these involve one or both of the loops folding back on itself. Sections of the hind gut in the foot show a single typhlosole and although the typhlosole was not obvious in all sections, it could be seen in whole mounts as a ridge running along the complete length of the hind gut. Material in the gut consisted of soft clay with broken skeletal remains. Fragmented diatom and silicoflagellate frustules of several different species were observed. The stomach contents are looser and less compact than the material present in the hind gut.

The sexes are separate. The gonads overlie the lateral and dorsal sides of the hind gut loops and the digestive diverticula. As the gonads develop they first form a ring around the loop of the gut and when mature totally overlie the viscera laterally. The gonadial apertures lie dorsal and close to those of the kidney, immediately anterior to the posterior pedal retractor muscle. No gonad was observed in specimens below 1.6 mm in length but some development had occurred in all specimens above this length (Fig. 16). The ratio of males: females is approximately 1:1. The egg number varies with the size of the individual; approximately 100 eggs were observed in an individual 2.0 mm long while 380 eggs were observed in a specimen of 2.9 mm. Maximum observed length of an egg was 210 µm. Egg numbers and size were compared in two samples taken from a similar area and depth but four months apart (Table, Fig. 12). These perhaps indicate increasing maturity in the four months that separate the samples. The kidney is moderately large, highly ramified. It lies anterior to the posterior pedal retractor muscle and extends anteriorly on either side of the stomach, tapering towards the lateral pedal retractor muscles. A single layer of cuboid cells lines the kidney walls. A large pericaridial cavity lies dorsal and posterior to the stomach; the hind gut passes through this and the ventricle of the heart.

There is some variation in shell shape but variation of specimens within a population is no less that that between populations. A growth series (Fig. 13) shows that the adult shell becomes slightly more elongate with age and the rostrum becomes more prominent. Height to total length ratios and post-umbonal length to total length ratios (Fig. 14) verify visual observation. The size range of individual samples varies considerably. (Fig. 15) but there appears to be no relationship with increasing depth. This variation is probably related to sporadic settlements and is borne out in that population size frequency histograms show variable numbers of peaks within the size range (Fig. 16). These are not necessarily related to age classes but probably to the survival of particular spatfalls.

L. pustulosa appears to be closely related to *Ledella inopinata* Smith. The latter species has been recorded from the Southwest Pacific, off Australia (Smith 1885), off Celebes (Prashad 1932). However, it differs from the present species in its dentition, and grows to a larger size. The Pliocene fossil material from Southern Italy identified by Seguenza (1877) appears to have a prominant escutcheon and a thicker hinge plate and may be a distinct species (Fig. 17).

DISTRIBUTION. Northeastern Atlantic; Rockall; Bay of Biscay; Southwest of Ireland; Canaries. Lower Slope and Abyssal Rise.

DEPTH RANGE. of 58 samples – 609–2659 m, exceptionally two samples (not listed) appear to have been collected from deeper water—4706 m (Biogas IV CP17) and 4829 m (Incal WS03), but we are inclined to believe that this may have been due to incomplete washing of the sampling gear after earlier samples.

Ledella pustulosa marshalli new subspecies

HOLOTYPE. BM(NH) no. 1885.11.5.411 (Paralectotypes of *L. pustulosa*).

PARATYPE. USNM No. 199578 from same Station.

TYPE LOCALITY. Porcupine Expedition (1869) Station 31, 2487 m northwest of Ireland.

SYNONYMY. *Leda pustulosa* Jeffreys 1876 *Ann. Mag. nat Hist.* Ser. 18, *4*, p. 430 (in part).
Leda pustulosa Jeffreys: Jeffreys 1879 *Proc. Zool. Soc. Lond.* 1879, p. 576 (in part).

MATERIAL

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		WEST EUROPEAN BASIN					
Jean Charcot	DS20	4226	2	47°33.0′N	9°36.7′W	DS	24.10.72
(Polygas)	DS21	4190	1	47°31.5′N	9°40.7′W	DS	24.10.72
	DS28	4413	3	44°23.8′N	4°47.5′W	DS	2.11.72
(Biogas III)	DS41	3548	12	47°28.3′N	9°07.2′W	DS	26. 8.73
(Biogas IV)	DS53	4425	6	44°30.4′N	4°56.3′W	DS	19. 2.74
	DS55	4125	2	47°34.9′N	9°40.9′W	DS	22. 2.74
	DS57	2906	1	47°30.8′N	9°07.6′W	DS	23. 2.74
	DS58	2775	5	47°34.1′N	9°08.2′W	DS	23. 2.74

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
(Biogas V)	DS66	3480	1	47°28.2′N	9°0.00′W	DS	16. 6.74
	DS67	4150	1	47°31.0′N	9°35.0′W	DS	17. 6.74
(Biogas VI)	DS73	2805	1	47°32.1′N	9°06.0′W	DS	21.10.74
	DS74	2777 ·	1	47°33.0′N	9°07.8′W	DS	21.10.74
	DS76	4228	5	47°34.8′N	9°33.3′W	DS	23.10.74
	CP10	2878	4	47°29.6′N	9°04.5′W	CP	21.10.74
	CP13	4134	3	47°34.4′N	9°38.0′W	CP	23.10.74
	CP14	4287	1	47°32.0′N	9°35.9′W	CP	23.10.74
Chain 106	321	2890–2868	74	50°12.3′N	13°35.8′W	ES	20. 8.72
				−50°08.3′N	−13°53.7′W		
	323	3356–3338	18	50°08.3′N	13°50.9′W	ES	21. 8.72
				−50°04.9′N	−14°23.8′W		
	326	3859	12	50°05.3′N	14°24.8′W	ES	22. 8.72
	330	4632	1	50°43.5′N	17°51.7′W	ES	24. 8.72
				−50°43.4′N	−17°52.9′W		
Jean Charcot (INCAL)	CP03	2466	14	56°38.0′N	11°06.4′W	CP	17. 7.76
				−56°37.3′N	−11°07.8′W		
	CP04	2483–2513	17	56°33.2′N	11°11.3′W	CP	17. 7.76
				−56°32.5′N	−11°12.4′W		
	DS05	2503	92	56°28.1′N	11°11.7′W	DS	18. 7.76
				−56°27.6′N	−11°12.0′W		
	DS06	2494	99	56°26.6′N	11°10.5′W	DS	18. 7.76
				−56°25.9′N	−11°10.7′W		
	DS07	2884	500	55°00.7′N	12°31.0′W	DS	19. 7.76
				−55°01.0′N	−12°32.0′W		
	DS08	2891–2884	57	55°02.0′N	12°34.6′W	DS	19. 7.76
				−55°01.9′N	−12°33.4′W		
	CP05	2884	222	55°00.4′N	12°29.4′W	CP	19. 7.76
				−55°00.9′N	−12°31.1′W		
	CP06	2888–2893	408	55°02.3′N	12°40.3′W	CP	19. 7.76
				−55°02.6′N	−12°41.7′W		
	CP07	2895	657	55°03.4′N	12°46.2′W	CP	20. 7.76
				−55°04.4′N	−12°46.7′W		
	DS09	2897	1280	55°07.7′N	12°52.6′W	DS	20. 7.76
				−55°08.1′N	−12°53.2′W		
	CP08	2644	6	50°14.7′N	13°13.5′W	CP	27. 7.76
				−50°15.2′N	−13°14.8′W		
	CP09	2659–2691	2	50°15.4′N	13°15.8′W	CP	27. 7.76
				−50°14.3′N	−13°16.1′W		
	DS10	2719	1	50°12.7′N	13°16.6′W	DS	27. 7.76
				−50°13.2′N	−13°16.4′W		
	0S01	2634	4	50°14.4′N	13°10.9′W	OS	30. 7.76
				−50°15.2′N	−13°11.0′W		
	0S04	4796	1	46°03.9′N	10°12.8′W	OS	5. 8.76
					−10°11.6′W		
	WS07	4281–4274	4	47°30.6′N	9°37.1′W	WS	7. 8.76
				−47°31.2′N	− 9°35.7′W		
	DS14	4254–4248	1	47°32.6′N	9°35.7′W	DS	7. 8.76
				−47°32.9′N	− 9°35.1′W		
	0S06	4316–4307	1	46°27.3′N	9°36.2′W	OS	9. 8.76
				−47°29.9′N	− 9°36.0′W		
	DS16	4268	4	47°29.8′N	9°33.4′W	DS	9. 8.76
				−37°30.3′N	− 9°33.4′W		
	WS09	4277	1	47°28.8′N	9°34.0′W	WS	10. 8.76
				−47°27.9′N	− 9°34.0′W		
	WS10	4354	2	47°27.3′N	9°39.9′W	WS	11. 8.76
				−47°28.2′N			
	0S08	4327	11	47°29.8′N	9°39.2′W	OS	11. 8.76
				−47°29.5′N	− 9°38.8′W		

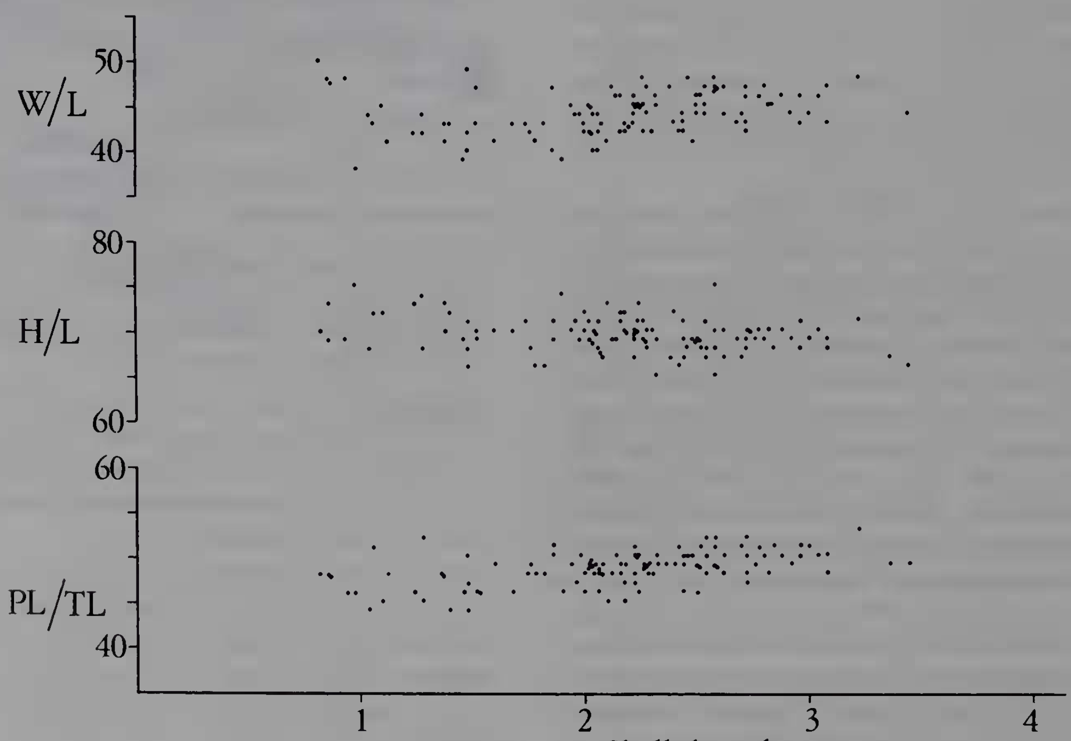

Fig. 14 *L. pustulosa pustulosa*: An analysis of change in shape with growth as shown by the plots, posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) all plotted against length.

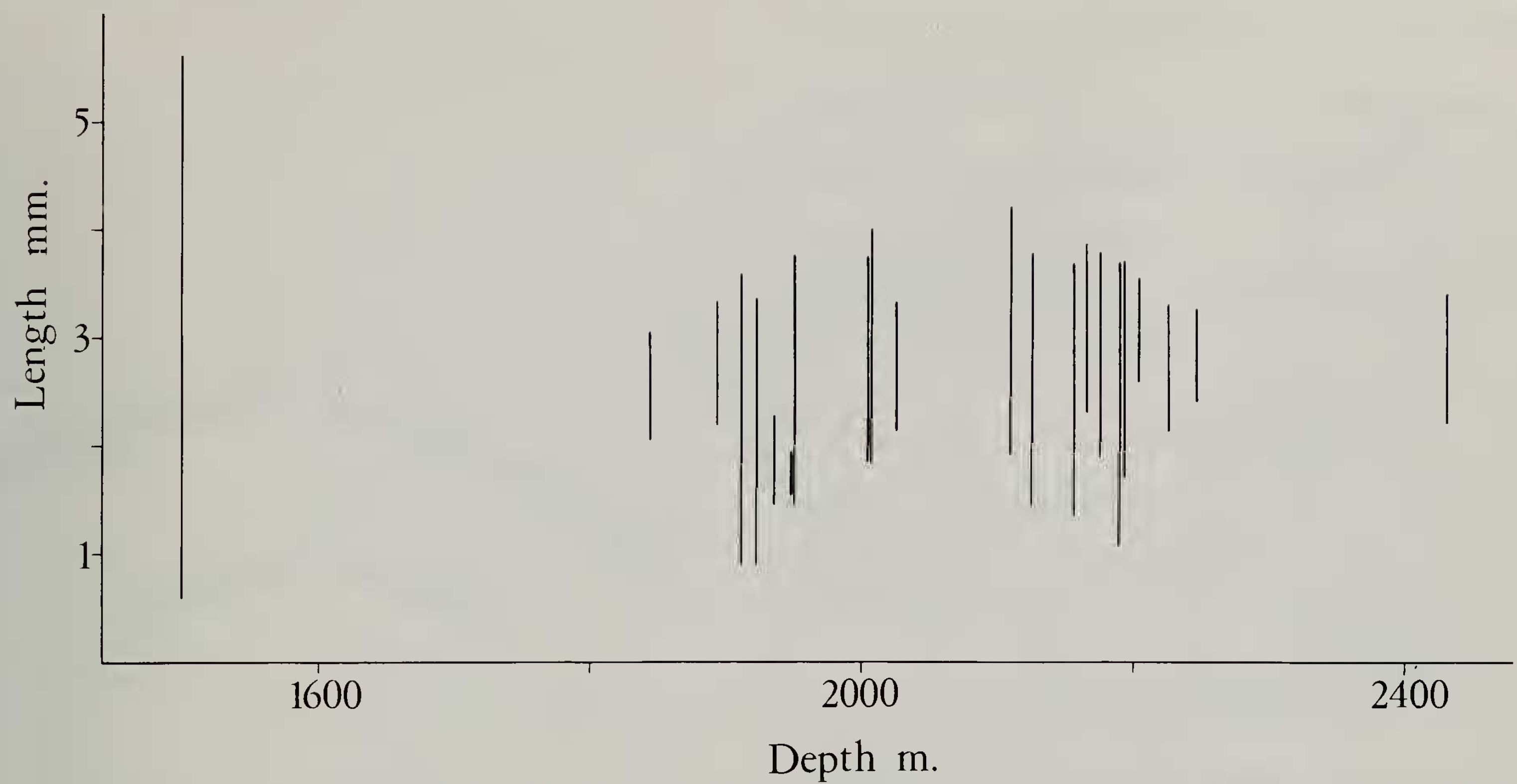

Fig. 15 *L. pustulosa pustulosa*: The range of shell lengths in individual samples taken with an epibenthic sledge plotted against Station depth.

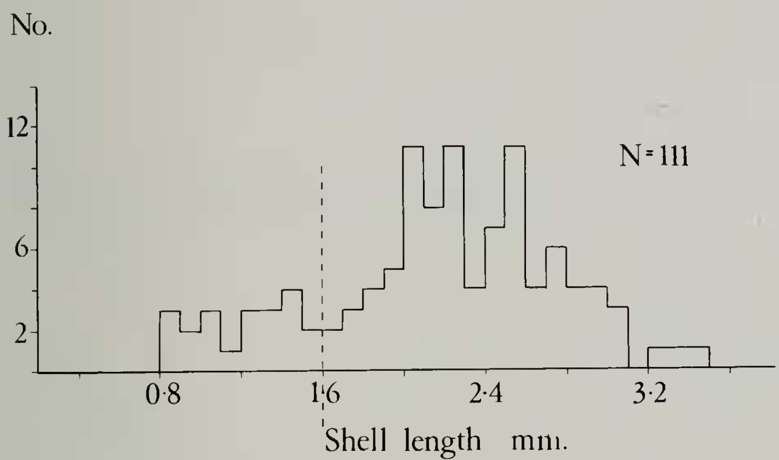

Fig. 16 *L. pustulosa pustulosa*: Length frequency histogram of specimens taken at Station Biogas VI DS87. The dashed line marks the minimum size at which gonadial development was observed.

DESCRIPTION (Figs 18a & b). Shell, similar to *L. p. pustulosa* but differs in being slightly more inflated, the overall lateral outline squarer and more 'angular', anterior and posterior dorsal margin proximally straight, dorsal anterior margin curves sharply into broadly curved anterior margin, posterior dorsal margin continuous curve with dorsal margin of rostrum, tip of rostrum more ventral in position than in *L. p. pustulosa*, posterior ventral margin more deeply sinuous than in *L. p. pustulosa*.

In general *L. p. marshalli* appears to have fewer, broader teeth (range: 5–10 on either side of resilium) than *L. p. pustulosa* (but see p. 125 Fig. 2a)

Larval shell length 245 μm; maximum observed length 5.06 mm.

The internal morphology is virtually undistinguishable from that of *L. p. pustulosa* (Fig. 19). The number of gill filaments and labial palp ridges are of the same order in both subspecies. *L. p. marshalli* possibly has slightly longer gill filaments and larger, broader palp ridges, and the byssal gland appears to be larger. The latter may have some

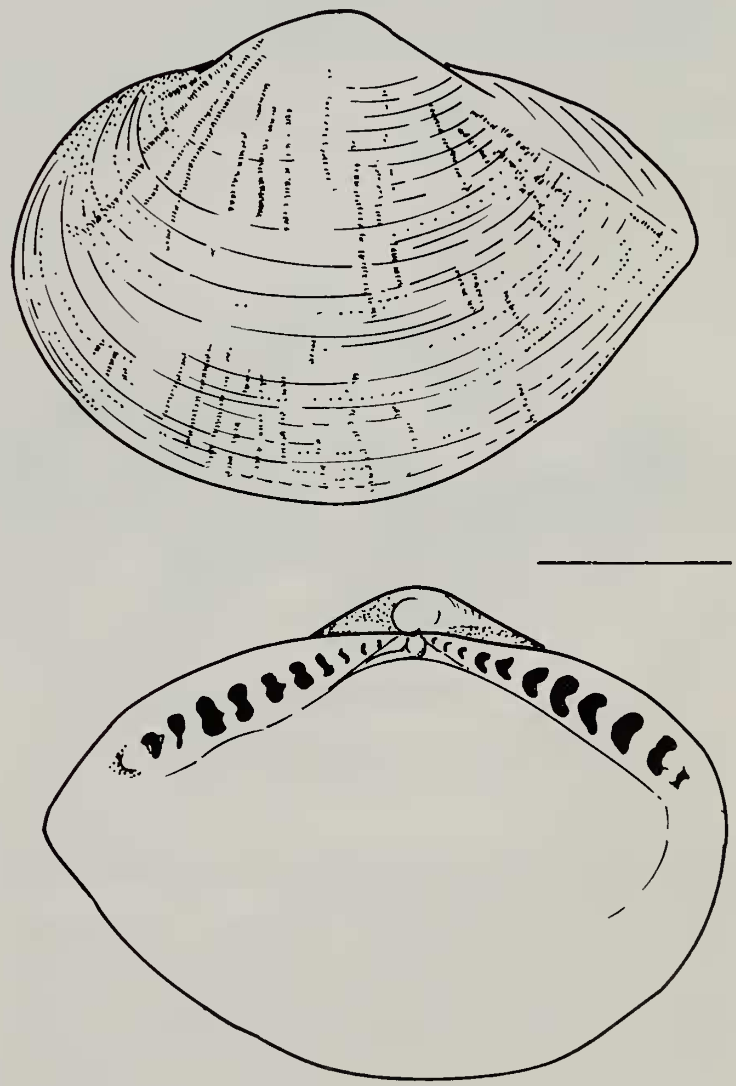

Fig. 17 Specimen No. 199587 from the U.S. National Museum labelled 'Ledella pustulosa (Jeff)', Messina Sicily, Seguenza fossil. (Scale = 1 mm).

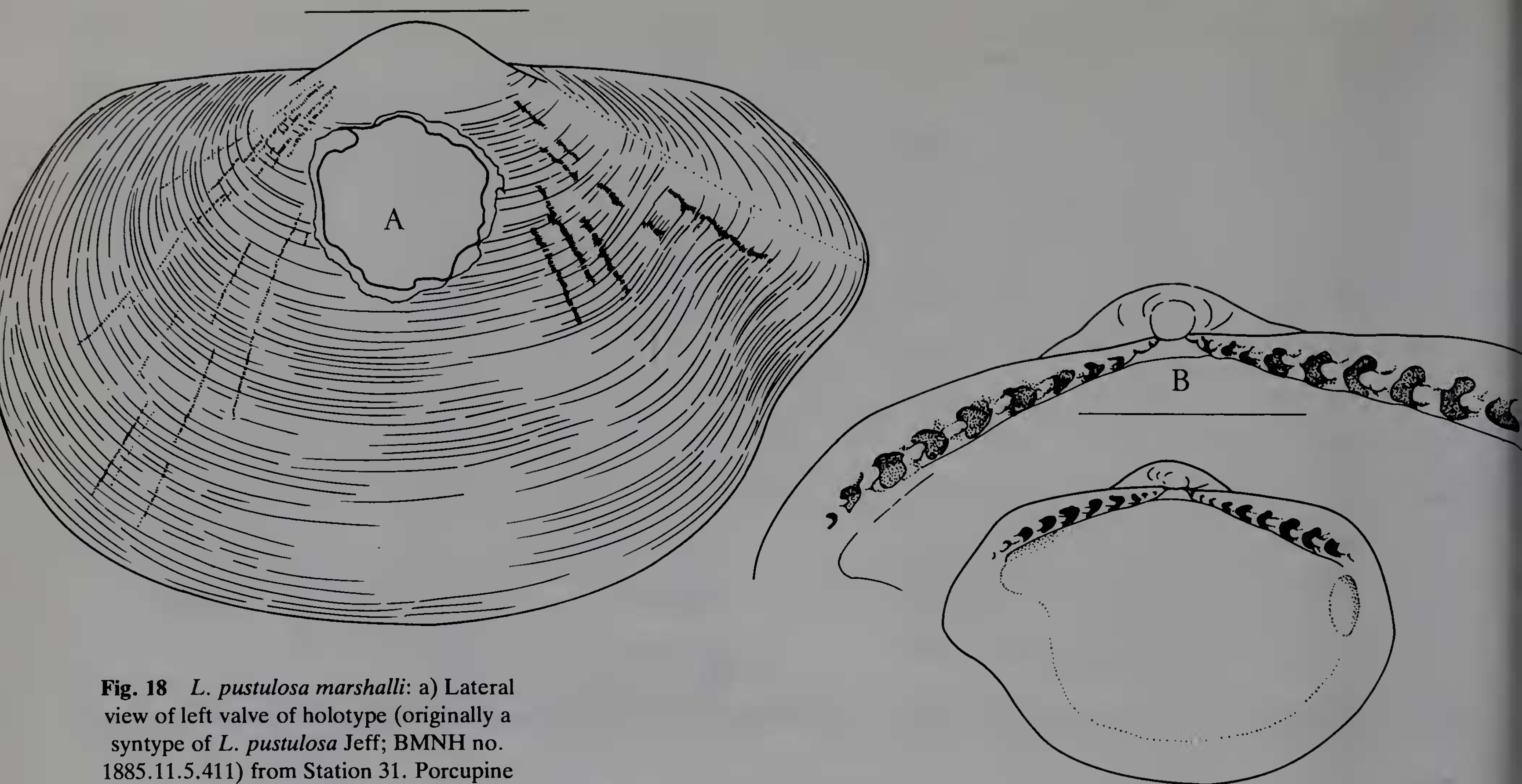

Fig. 18 *L. pustulosa marshalli*: a) Lateral view of left valve of holotype (originally a syntype of *L. pustulosa* Jeff; BMNH no. 1885.11.5.411) from Station 31. Porcupine Expedition, 1360 fathoms, N.W. of Ireland; b) Internal view of same valve with enlarged detail of hinge plate. (Scales = 1 mm).

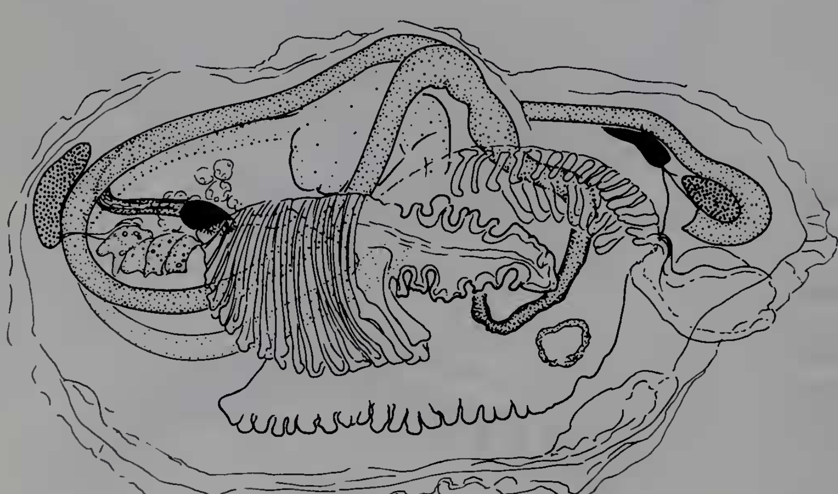

Fig. 19 *L. pustulosa marshalli*: Lateral view of specimen from the left side with shell removed to show arrangement of body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

significance in that generally nuculanoids from deeper depths appear to have larger 'byssal' glands.

Examination of the maturity of individuals of a subsample of *L. p. marshalli* (Incal DS09) shows no gonadial development in specimens below 1.75 mm in length. As in *L. p. pustulosa*, the number of eggs increases with the length of the adult. Thus, there was 59 (maximum egg diameter 120 μm) present in an individual 2.14 mm long, 187 (max diameter 140 μm) in an individual 3.18 mm long while a still larger female (4.13 mm) had 318 eggs although these were at an earlier stage in development (max diameter 85 μm). This possibly suggests that the species breeds more than once in its life and that breeding is not synchronous.

In the course of growth, the rostrum becomes more pronounced and the posterior ventral sinuosity more concave (Fig. 20). As a result of the proportionate change in growth, the umbo becomes more central, lying immediately posterior to the mid point and the height/length ratio decreases from a mean value of 0.76 to a mean value of 0.69. The width-length ratio is maintained within the range 0.4–0.5.

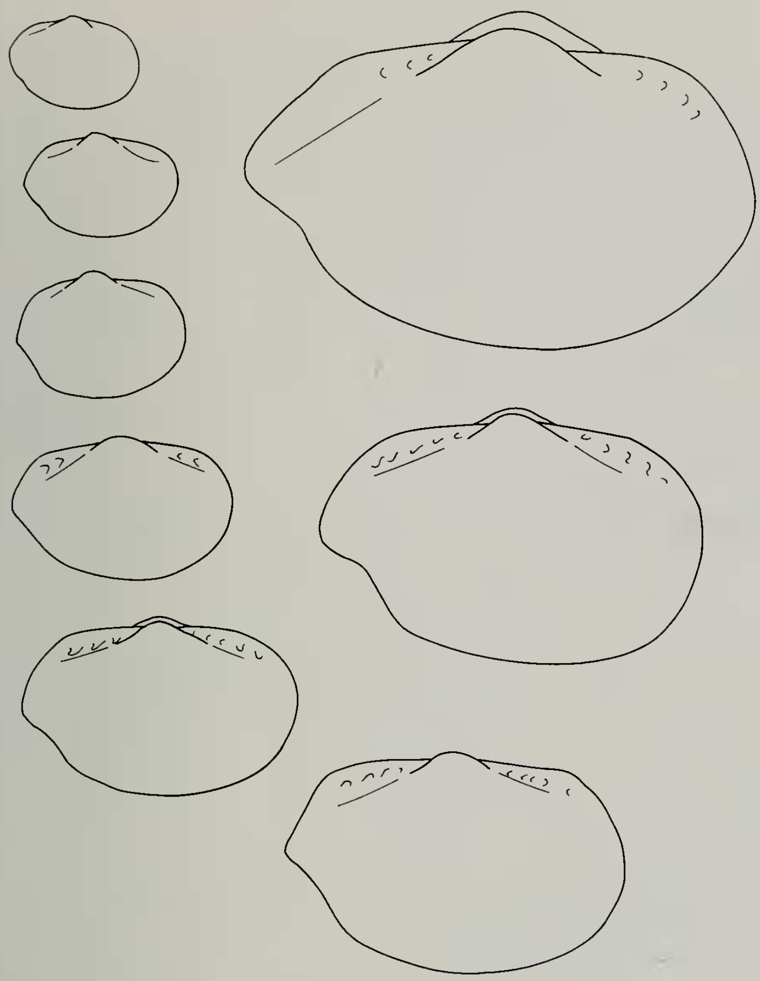

Fig. 20 *L. pustulosa marshalli*: Growth series of shells from Station 321 seen in outline from right side.

DISTRIBUTION. West European Basin—Rockall, Bay of Biscay, Southwest of Ireland. Abyssal rise to deepest abyssal depths.

DEPTH RANGE. 2466–4796 metres.

Ledella pustulosa argentinae new subspecies

HOLOTYPE. BM(NH) 1988084

TYPE LOCALITY. Station 247, Atlantis II, Cruise 60, 5208–5223 m, Argentine Basin.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
				ARGENTINE BASIN			
Atlantis II	242	4382–4402	104	38°16.9′S	51°56.1′W	ES	13. 3.71
60	243	3820	41	37°36.8′S	52°23.6′W	ES	14. 3.71
	247	5208–5223	57	43°33.0′S	48°58.1′W	ES	17. 3.71
	256	3906–3917	97	37°40.9′S	52°19.3′W	ES	24. 3.71
	259	3305–3317	6	37°13.3′S	52°45.0′W	ES	26. 3.71

DESCRIPTION (Fig. 22). Shell, similar in shape to *L. p. marshalli*, surface more smooth with less conspicuous concentric ridges and radial striae, shell of valves slightly thicker, umbo more central, slightly more inflated; number of hinge teeth appear to intermediate between *L. p. pustulosa* and *L. p. marshalli*, however there was no significant difference between the teeth number/length measurements of the three subspecies.

Larval shell length 240 μm, maximum recorded length 4.74 mm.

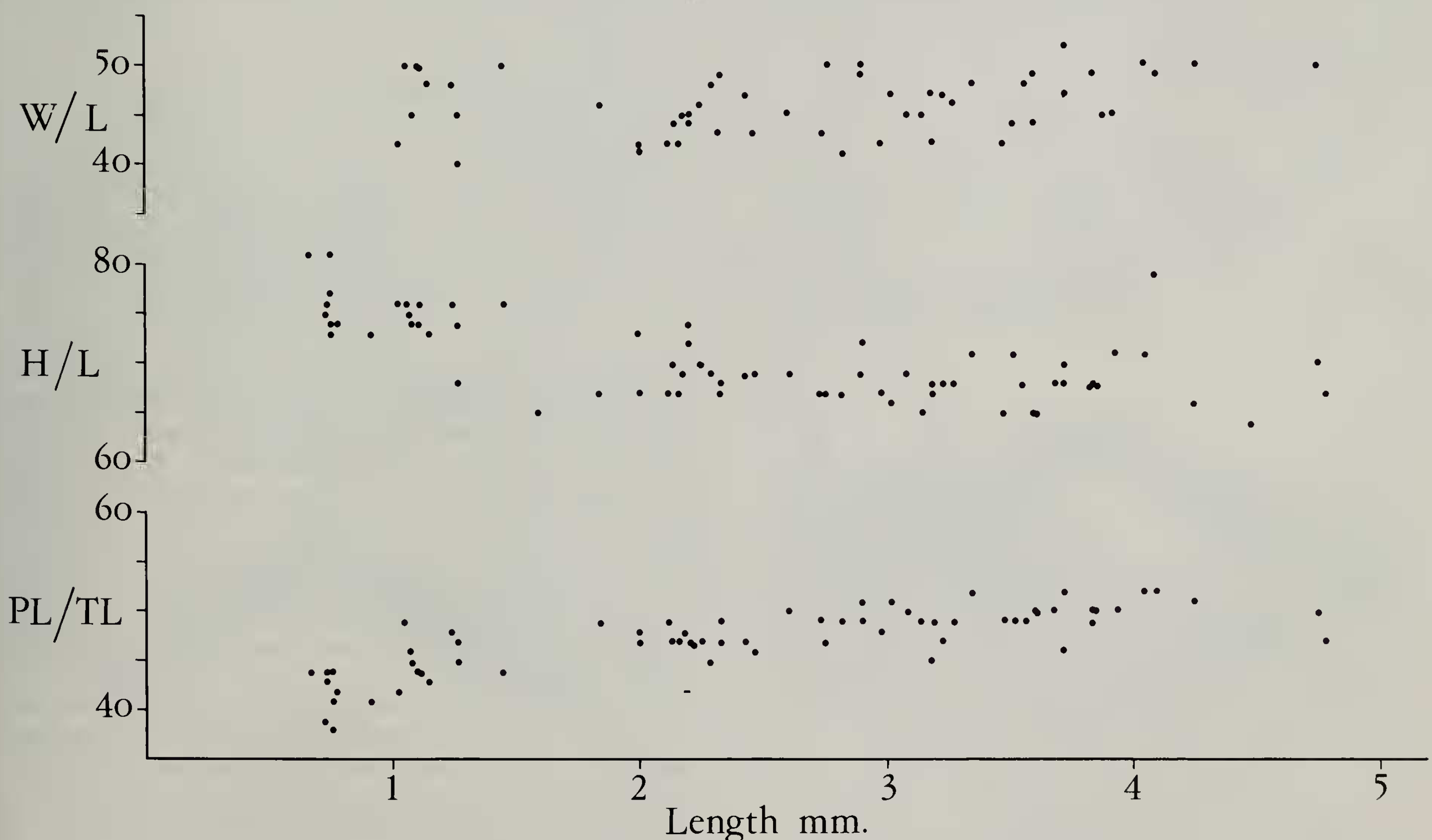

Fig. 21 *L. pustulosa marshalli*: An analysis of change in shape with growth as shown by the plots of the ratios, post-umbo length/length (PL/TL); height/length (H/L) and width/length (W/L) against length for specimens from Sta. 321.

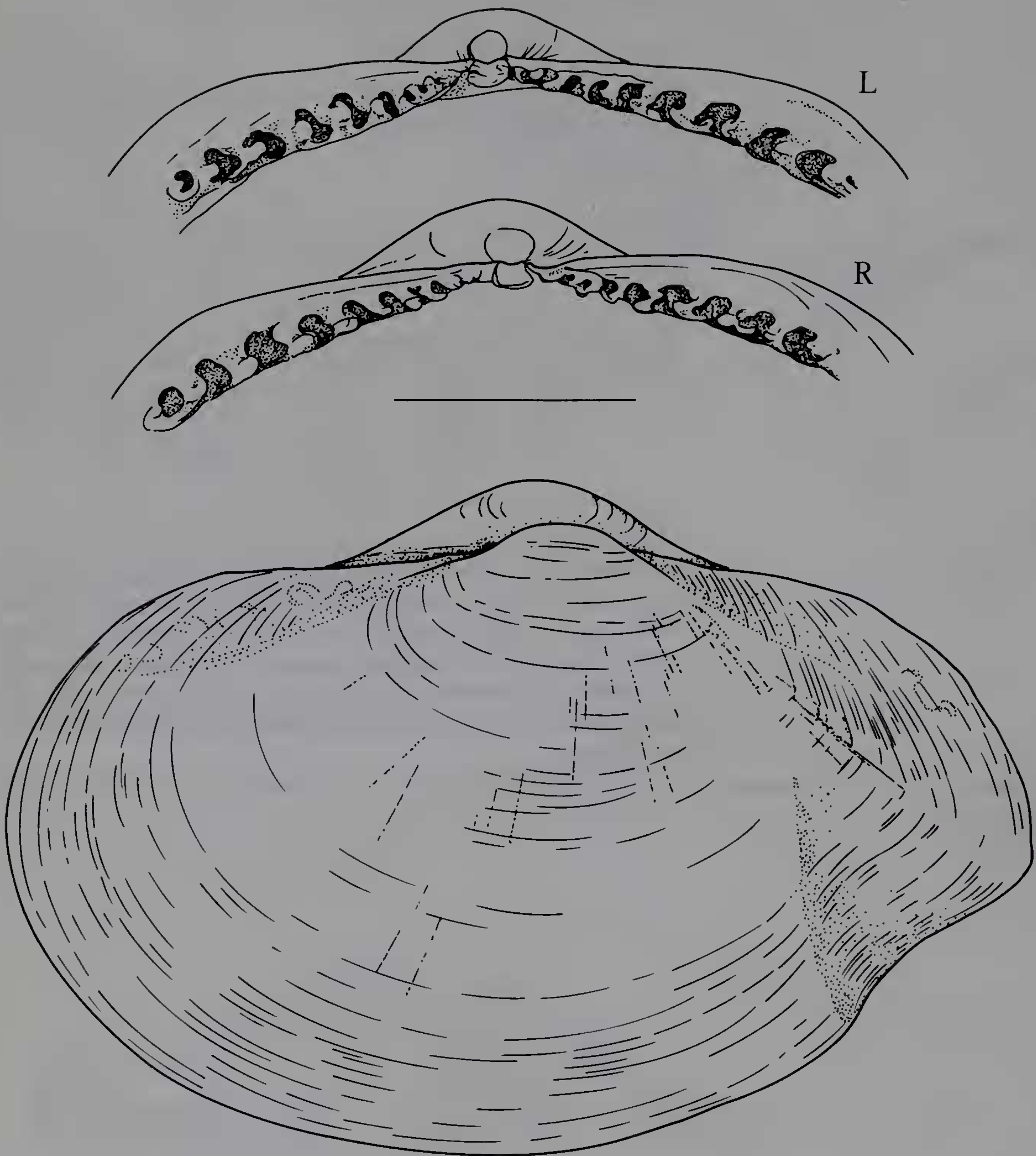

Fig. 22 *L. pustulosa argentinae*: Left lateral view of shell from Atlantis II, Sta. 247, and detail of hinge plates of right and left valves of the holotype. (Scale = 1 mm).

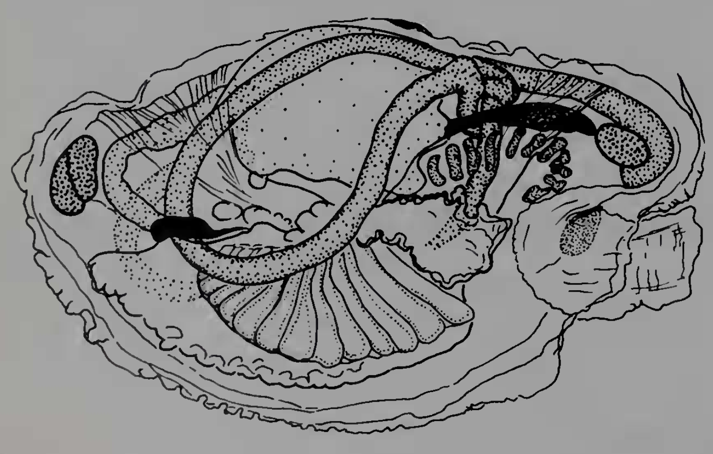

Fig. 23 *L. pustulosa argentinae*: Lateral view of specimen from left side with shell removed to show arrangement of body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

The basic body form while similar to that of *L. p. pustulosa* has several slight differences (Fig. 23). The adductor muscles are larger and the posterior, in particular, is more rounded in outline than in the previously two subspecies. The labial palps have fewer (7–12) but broader ridges and the number of gill filaments (8–13) is also less. Posterior to the foot, the inner demibranchs appear to interlock and provide a channel for the faeces between the anus and siphon. There is a large byssal gland. The nervous system is well developed with large visceral and cerebral ganglia. The pedal ganglia are also large and lie high in the foot.

The smallest specimen seen with developing gonads was 1.9 mm long. The ova number varies from 55 (2.1 mm total length) to 169 (4.4 mm total length) and the egg lengths within the individual containing the largest ova varied from 150–180 μm. In this individual (3.00 mm total length), some eggs had been released and were lying cradled in the gill filaments close to the siphon.

In the course of growth, the anterior margin becomes more

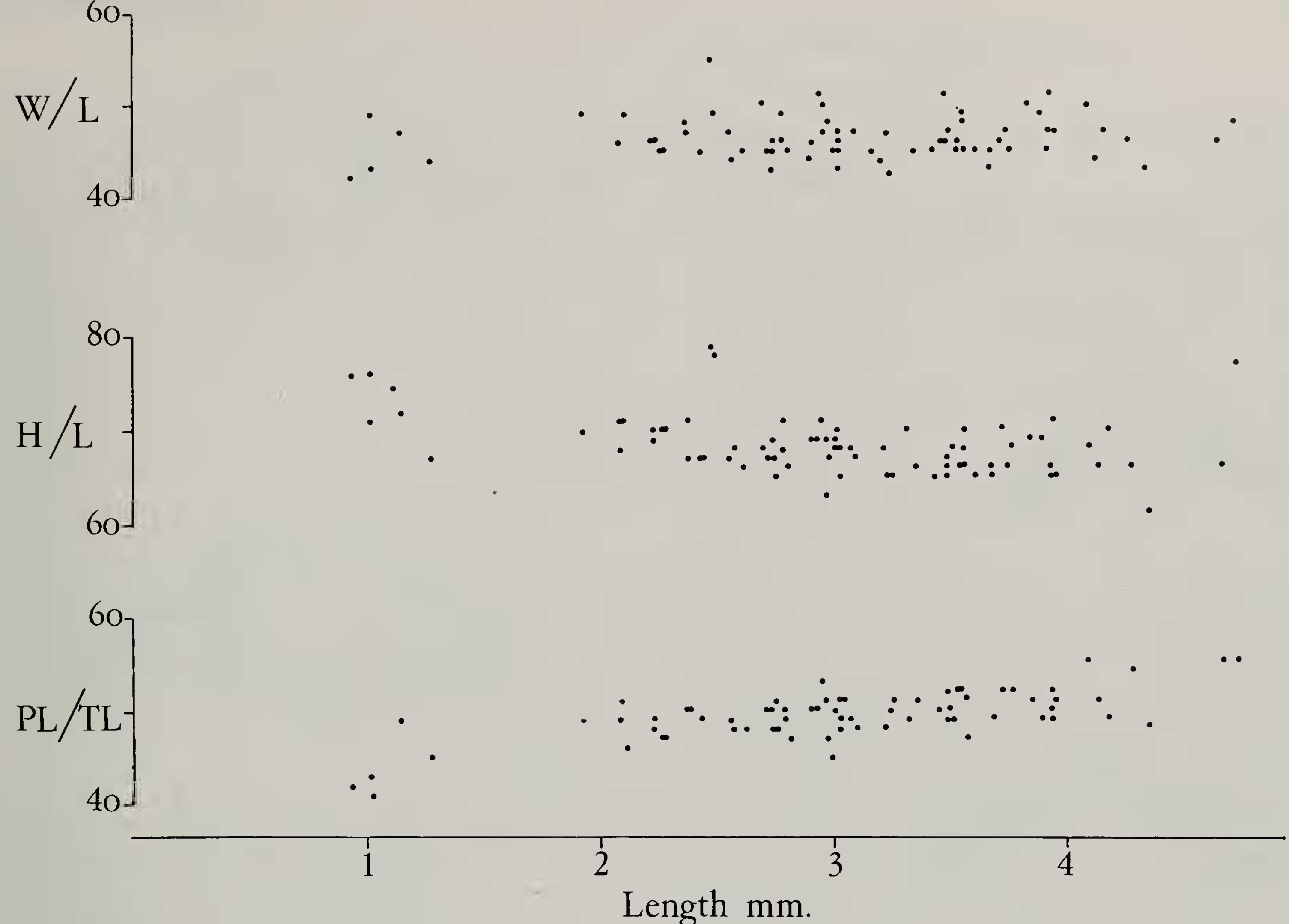

Fig. 24 *L. pustulosa argentinae*: An analysis of change in shape with growth as shown by the ratios, post-umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 242.

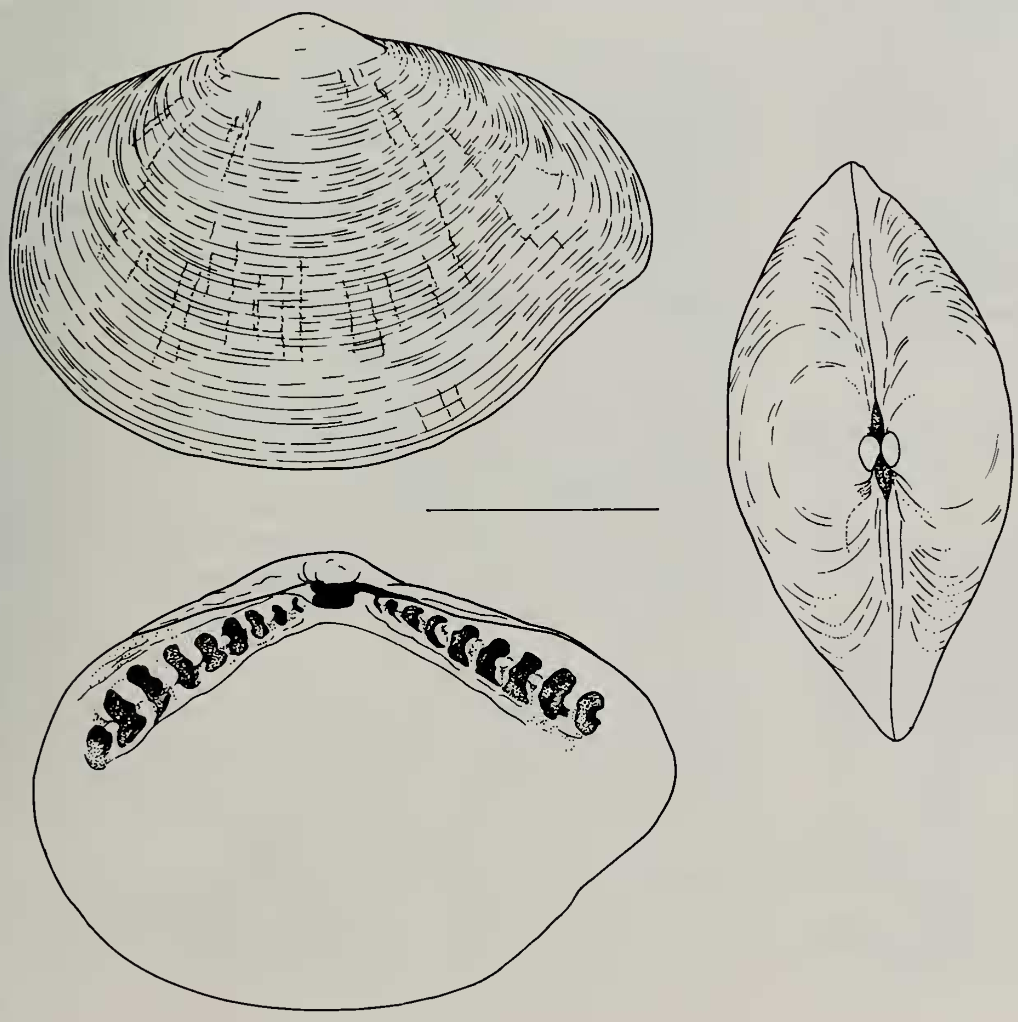

Fig. 25 *L. pustulosa hamsoni*: Left lateral external view of shell from Atlantis II, Station 144, lateral view of right valve of same shell and dorsal view of shell from Atlantis II, Station 141. (Scale = 1 mm).

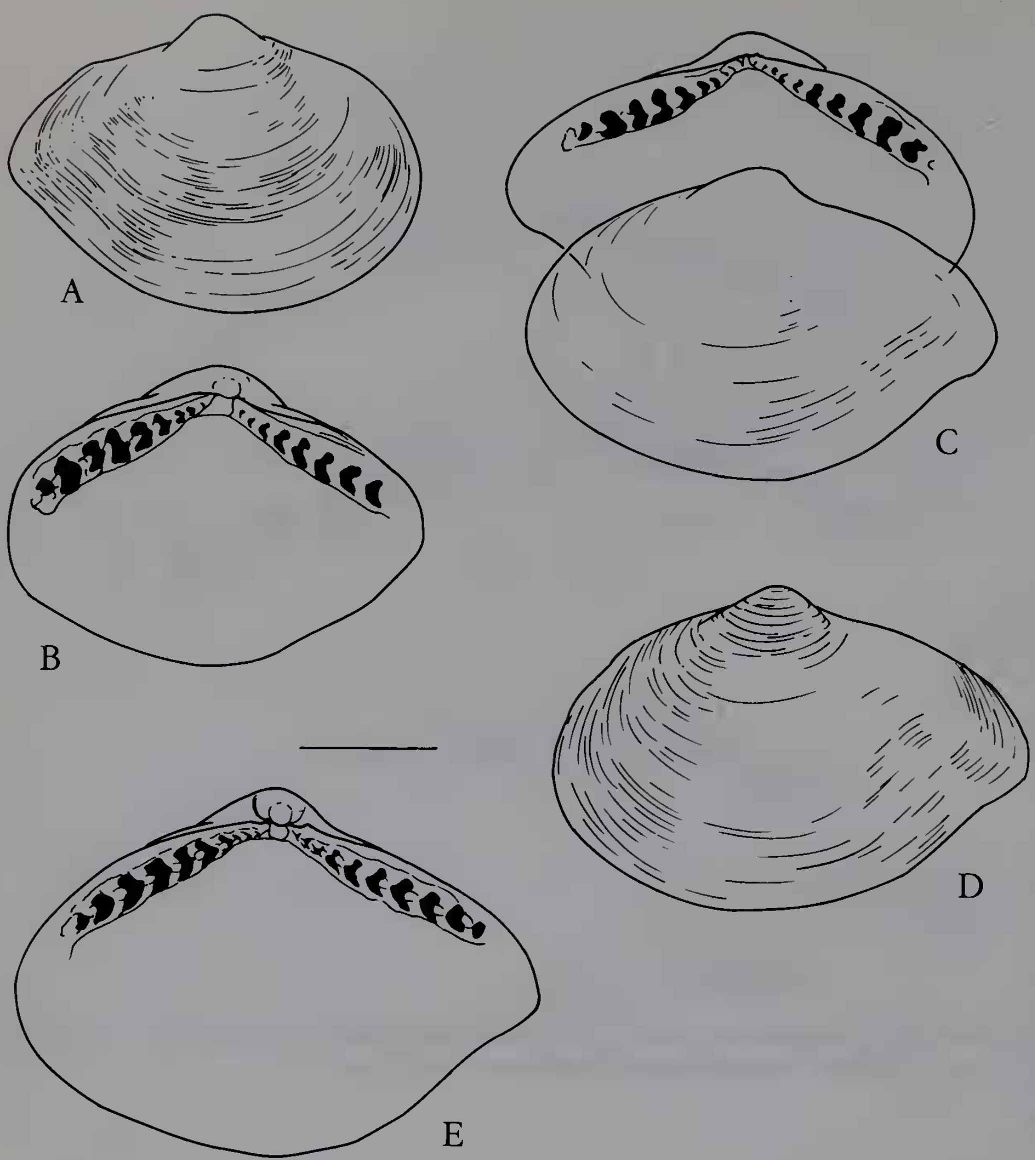

Fig. 26 *Ledella sublevis*: a) Lateral external view of holotype specimen (USNM No. 35212) as seen from right side; b) Lateral internal view of right valve of same specimen; c) Lateral external view and internal view of left valve of specimen (USNM No. 199689) labelled *Leda acuminata* but relabelled *Ledella sublevis* by Warén; d) Left lateral view of shell from Station Biogas III DS41, and e) Internal view of left valve of specimen from Station 262. (Scale = 1 mm).

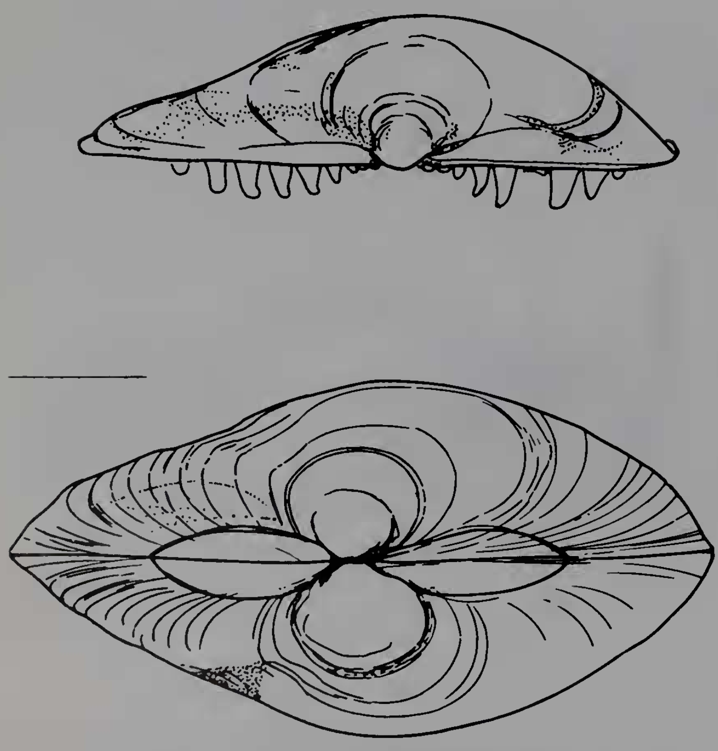

Fig. 27 *Ledella sublevis*: Dorsal view of an intact shell and a left valve from Station Biogas III DS41. (Scale = 1 mm).

smoothly curved and the ventral sinuosity more pronounced. The ratios of height/length, width/length and posterior umbonal distance/total length against length of this subspecies are similar to those of *L. p. pustulosa* and *L. p. marshalli* (Fig. 24).

DISTRIBUTION. Argentine Basin. Abyssal depths.

DEPTH RANGE. 3305–5223 metres.

Ledella pustulosa hampsoni new subspecies

HOLOTYPE. BM(NH) 1988085

TYPE LOCALITY. Station 144, Atlantis II, cruise 31, 2052–2357 m, 10°36.0′N 17°49.0′W, off West Africa.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		CAPE VERDE BASIN					
Atlantis II	141	2131	2	10°30.0′N	17°51.5′W	ES	5.2.67
31	144	2051–2357	3	10°36.0′N	17°40.0′W	ES	5.2.67
	145	2105–2192	1	10°36.0′N	17°49.0′W	ES	6.2.67

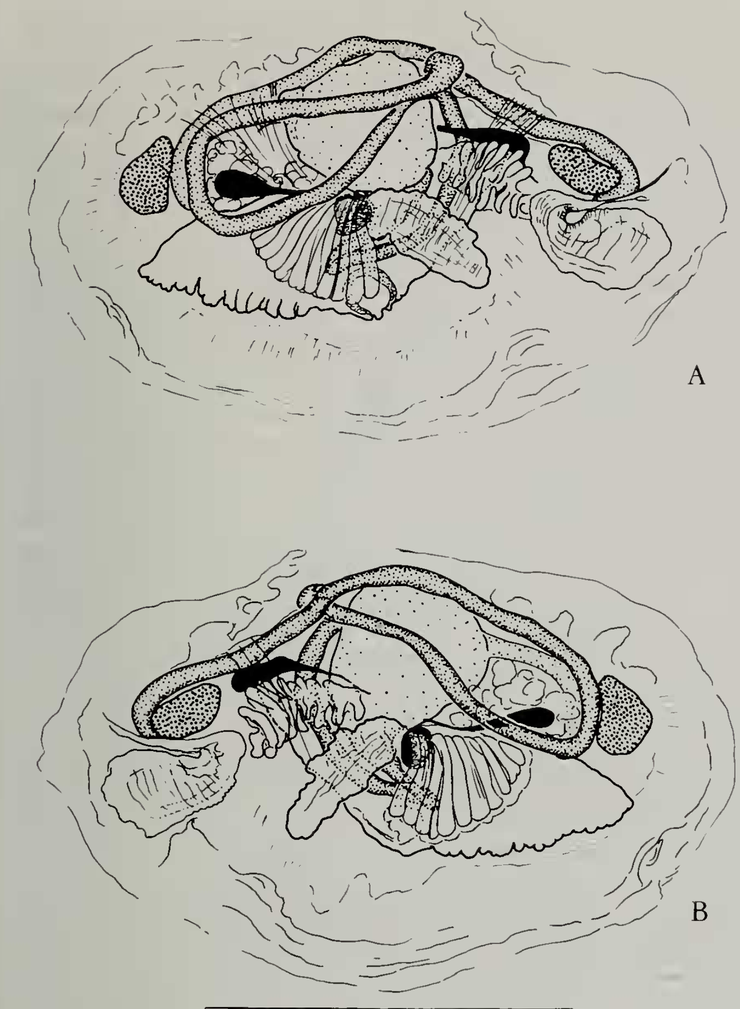

Fig. 28 *Ledella sublevis*: Lateral views of specimen from (a) left and (b) right sides with shell removed to show arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

DESCRIPTION (Fig. 25). Shell shape while variable most closely resembles *L. p. pustulosa*, radial striae present, more conspicuous and irregular concentric ridges than other subspecies, also shell of valves much thicker, stronger; broader hinge plate; unlike other subspecies internal ligament approximately rectangular in shape, restricted to upper half of hinge plate with small external part on either side of the beaks.

Larval shell length 150 μm, maximum recorded length 2.67 mm.

The shape of the hinge of this subspecies resembles that of the fossil described by Seguenza (1877) (Fig. 17). Because of the small number of specimens available only a limited comparison of the internal morphology with *L. p. pustulosa* was possible. The byssal gland is relatively small; there are 10–12 gill filaments and 10–14 palp ridges. The hind gut configuration is similar with loop on either side of the body. The visceral and cerebral ganglia are moderately small and club-shaped.

Gonads were not seen in an individual 1.7 mm in length but could be seen in an individual 2.2 mm in length. In the latter specimen the testis partially surrounds the hind gut loops and the digestive diverticula and lies dorsal to the viscera between the anterior adductor muscle and the resilium.

DISTRIBUTION. Off the West coast of Africa. Abyssal rise.

DEPTH RANGE. 2051–2357 metres.

Ledella sublevis Verrill & Bush, 1898

HOLOTYPE. USNM No. 35212.

TYPE LOCALITY. U.S. Fish Comm. Sta. 2689, off Martha's Vineyard, 960 m.

SYNONYMY. *Leda acuminata* Jeffreys, 1870 (in part) *Ann. Mag. nat. Hist.* Ser. 4, *6*, p. 69.
Leda messanensis Jeffreys, 1879 (in part). *Proc. zool. Soc. Lond.* p. 576.
Ledella messanensis var *sublevis* Verrill & Bush, 1898. *Proc. U.S. natl., Mus., 20*, p. 856, pl. 81, Fig. 7.
Leda (Ledella) modesta Thiele & Jaeckel, 1931. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*, 21, p. 44, pl. 2. Fig. 50.
Ledella ultima (Smith): Knudsen, 1970. *Galathea Rept., 11*, p. 34, Figs. 17 & 18, pl. 2, Fig. 15, pl. 3. Fig. 4.
Ledella sublaevis (Verrill & Bush): Warén, 1978. *Sarsia, 63*, p. 214, Figs. 14 & 15.

This species has been much confused with *L. ultima* (p. 155) and *L. acuminata* (p. 153). Indeed, Verrill (1884) and Verrill & Bush (1887, 1898) who recognized differences from *L. ultima* (*L. messanensis* as they thought) were not entirely sure and persisted in referring to the species as a variety. This was largely because there were very few specimens of *L. sublevis* present among many of *L. ultima* in mixed samples. Unfortunately they did not examine the morphology of the body organs. Curiously, even Knudsen (1970) who did examine the body considered that *L. modesta, L. ultima* and his specimen of *L. sublaevis* from the 'Galathea' Expedition to be conspecific. Having examined the types of *L. ultima* and *L. modesta* we disagree. The latter is without doubt distinct species however, *L. modesta* is conspecific with *L. sublevis*. The identification of the 'Galathea' specimen is somewhat unclear, but from Knudsen's description it would appear to us to be *L. sublevis*. Clarke (1961b) who also combined *L. modesta* with *L. ultima* additionally included *L. spreta* (Thiele & Jaeckel 1931) in his synonomy. His description agrees closely with that of *L. ultima* (Smith) and with our extensive collections of *L. ultima*. Having examined specimens of *L. spreta*, like Knudsen (1970) and Barnard (1964) before him, we consider it to be a separate species. We confirm the description by Warén (1978) and agree with him in raising the Verrill & Bush variety to species status but, correct his spelling to that of the original. The drawings by Warén (1978) are excellent in their accuracy.

MATERIAL. USNM No. 199689 labelled *Leda acuminata* (figured by Warén, 1978).

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		WEST EUROPEAN BASIN					
Sarsia	S50	2379	6	43°46.7′N	3°38.0′W	ED	18. 7.67
Chain 106	321	2868–2890	3	50°12.3′N −50°08.3′N	13°35.8′W −13°53.7′W	ES	20. 8.72
	323	3356–3338	4	50°08.3′N −50°04.9′N	13°50.9′W −14°23.8′W	ES	21. 8.72
	326	3859	12	50°05.3′N	14°24.8′W	ES	22. 8.72
	330	4632	1	50°43.5′N −50°43.4′N	17°51.7′W −17°52.9′W	ES	24. 8.72
Jean Charcot (Biogas III)	DS38	2138	2	47°32.5′N	8°35.8′W	DS	25. 8.73
	DS41	3548	22	47°28.3′N	9°07.2′W	DS	26. 8.73
(Biogas IV)	DS57	2906	2	47°30.8′N	9°07.6′W	DS	23. 2.74

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	DS60	3742	6	47°26.8′N	9°07.2′W	DS	24. 2.74
	DS63	2126	1	47°32.8′N	8°35.0′W	DS	26. 2.74
	CP01	2245	1	47°34.6′N	8°38.8′W	CP	25. 2.74
(Biogas V)	DS66	3480	1	47°28.2′N	9°00.0′W	DS	16. 6.74
(Biogas VI)	DS73	2805	1	47°32.1′N	9°06.0′W	DS	21.10.74
				GUINEA BASIN/SIERRA LEONE BASIN			
(Walda)	DS20	2514	1	2°32.0′S	8°18.1′E	DS	
	DS25	2470	34	2°19.8′S	7°49.2′E	DS	
				NORTH AMERICA BASIN			
Atlantis 273	GH*2	2488	1	39°26.0′N	70°34.0′W	AD	3.10.61
Atlantis II 12	62	2496	3	39°26.0′N	70°33.0′W	ES	21. 8.64
	64	2886	7	38°46.0′N	70°06.0′W	ES	21. 8.64
	70	4680	1	36°23.0′N	67°58.0′W	ES	23. 8.64
	72	2864	6	38°16.0′N	71°47.0′W	ES	24. 8.64
Chain-50	76	2862	10	39°38.3′N	67°57.8′W	ES	29. 6.65
	85	3834	3	37°59.2′N −39°37.0′N	69°26.2′W −66°47.0′W	ES	5. 7.65
Chain-58	103	2022	4	39°43.6′N	70°37.4′W	ET	4. 5.66
	115	2031–2051	1	39°39.2′N	70°24.5′W	ET	16. 8.66
Atlantis II 24	126	3806	8	39°37.0′N −39°37.5′N	66°47.0′W −66°44.0′W	ES	24. 8.66
Atlantis II 30	131	2178	22	39°38.5′N −39°39.0′N	70°36.5′W −70°37.1′W	ES	18.12.66
	340	3264–3356	15	38°14.4′N −38°17.6′N	70°20.3′W −70°22.8′W	ES	24.11.73
				CAPE VERDE BASIN			
Atlantis II 31	147	293	27	10°38.0′N	17°52.0′W	ES	6. 2.67
				ARGENTINE BASIN			
Atlantis II 60	239	1661–1679	142	36°49.0′S	53°15.4′W	ES	11. 3.71
	140	2195–2323	18	36°53.4′S	53°10.2′W	ES	12. 3.71
	245	2707	8	36°55.7′S	53°01.4′W	ES	14. 3.71
	259	3305–3317	24	37°13.3′S	52°45.0′W	ES	26. 3.71
	262	2440–2480	220	36°05.2′S	52°17.9′W	ES	27. 3.71
	264	2041–2048	2	36°12.7′S	52°42.7′W	ES	28. 3.71
				ANGOLA BASIN			
Atlantis II 42	200	2644–2754	7	9°43.5′S − 9°29.0′S	10°57.0′E −11°34.0′E	ES	22. 7.68

DESCRIPTION (Figs. 26a-e, 27). Shell moderately thick, elongate, oval with pointed rostrum, sculpture fine regular concentric ridges more prominent ventrally, several radial striae or wrinkles usually visible in oblique rostral depression; dorsal margin moderately convex, antero-dorsal margin slopes gradually from umbo to form smooth curve with anterior margin proximal, postero-dorsal margin gradually slopes from umbo to posterior limit of hinge plate distally then more sharply to form rostrum, posterior ventral margin sinuous, ventral margin smooth, moderately convex curve; umbo inflated, slightly inclined posteriorly, relatively more anterior in position in large specimens; keel extends from umbo to rostral tip, concentric ridges curve acutely at this point; hinge plate long, broad, anterior and posterior series of 6–12 strong, upright chevron-shaped teeth, the number vary with size; ligament amphidetic, internal part moderately large, approximately as long as wide, trapezoidal with truncated apex, extending externally for short distance on either side of umbo; pallial and sinus scar conspicuous in large specimens.

MORPHOLOGY. *Ledella sublevis* has a similar morphology to *L. pustulosa* (Figs. 19 & 28a & b). Of the mantle structures, the wall of the combined siphon is thick and muscular with a well developed feeding aperture ventral to it. The siphonal tentacle originates on the left side of the siphonal embayment. The adductor muscles are almost equal in size, the anterior being the slightly larger.

The gills have approximately 14 plates to each demibranch. In this species they do not appear to interlock posterior to the foot but this may be a matter of change following fixation. The palps are small, with 12 ridges in the largest specimens.

There is a large 'byssal' gland in the heel of the foot. The large stomach has six sorting ridges, and together with the style sac, is similar to that described for *L. pustulosa*. The style sac penetrates the ventral half of the foot (Figs. 28a & b) and there are single loops of hind gut on each side of the body. The course of the hind gut differs somewhat from that of *L. pustulosa* in that having passed from the left side of the body to the right the gut takes an anterior and horizontal course for a short distance before forming the right loop.

The ganglia are well developed. The kidney is large with a ventral lobe penetrating the foot posterior to the style sac.

During growth the rostrum becomes more pronounced with a gradual increase in the umbo-rostral length/total length ratio with increasing length (Fig. 29). At the same time there is also a decrease in the height to length ratio with increasing length. There is little change in the width to length ratio.

The smallest specimen with developing gonads was 2.5 mm total length (Station 262, Argentine Basin). The sexes are separate, with males and females in approximately equal number. The number of ova increases from 102 (2.5 mm length) to 265 (4.2 mm length), but the maximum size of the ova varied little between individuals of different sizes (140–160 μm).

DISTRIBUTION. North East and West Atlantic and Argentine Basin.

DEPTH RANGE. 2022–4680 m.

This species differs from other species of *Ledella* in having a smoother, thicker, more inflated shell, in which the concentric ridging is much less pronounced. It is more elongate than *L. ultima* with a more pointed rostrum. Other characteristic features are the broad hinge plate and the small but clearly visible external part of the ligament. The type of gut configuration is similar to that of the *L. pustulosa* complex.

There are some population differences in the specimens from the Argentine basin as compared with elsewhere. While the internal morphology is identical externally the Argentine shells are slightly thinner and differ slightly in their shape, being somewhat more elongate, and in the thickness of the hinge plate and the form of the ligament, and but for the differences in internal morphology might be confused with *L. acuminata*.

Ledella jamesi new species

HOLOTYPE. BM(NH) 1988087

TYPE LOCALITY. Knorr 25, Station 299, 7°55.1′N, 55°43.0′W, 1942–2076 m, Guiana Basin.

SYNONYMY. *Nuculana A.* James 1972 Thesis, Texas A & M. Univ. p. 126. Figs. 79–81.

MATERIAL.

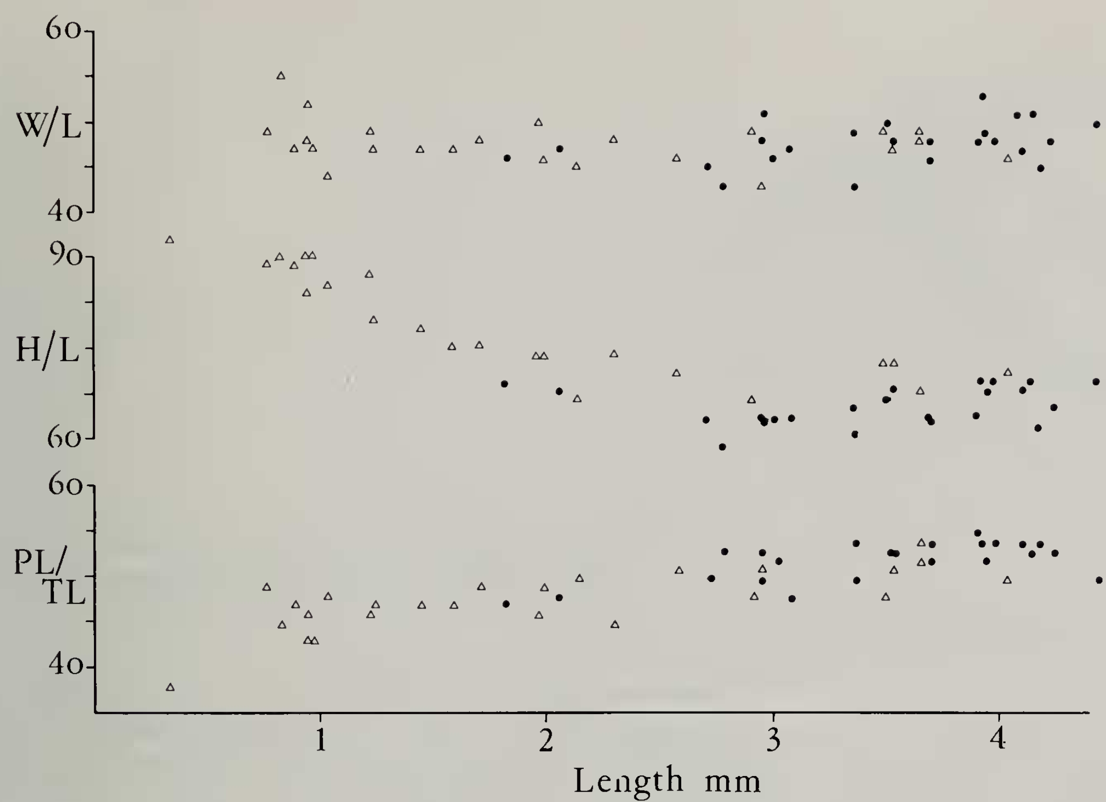

Fig. 29 *Ledella sublevis*: An analysis of change in shape with growth as shown by the ratios, posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Stations Walda DS25 (closed circles) and 259 (open triangles).

Cruise	Sta	Depth(m)	No	Lat.	Long.	Gear	Date
				ARGENTINE BASIN			
Atlantis II	239	1661–1679	889	36°49.0′S	53°15.4′W	ES	11. 3.71
60	240	2195–2323	61	36°53.4′S	53°10.2′W	ES	12. 3.71
	262	2440–2480	3	36°05.2′S	52°17.9′W	ES	27. 3.71
	264	2041–2048	8	36°12.7′S	52°42.7′W	ES	28. 3.71
				GUIANA BASIN			
Knorr 25	293	1456–1518	2	8°58.0′N	54°04.3′W	ES	27. 2.72
	299	1941–2076	566	7°55.1′N	55°42.0′W	ES	29. 2.72
	301	2487–2500	51	8°12.4′N	55°50.2′W	ES	29. 2.72
	303	2842–2853	268	8°28.8′N	56°04.5′W	ES	1. 3.72

James (1972) gives a description of valves of this species taken from depths of 752–527 m in the Gulf of Mexico, in her thesis on the protobranch molluscs from the deep waters of the Gulf.

Description (Figs. 30a & b). Shell inequilateral, moderately inflated, approximately oblong, somewhat variable in outline with short pointed rostrum, sculpture prominent, slightly irregular concentric ridges with radial striations in posterior depression in front of keel; umbo slightly posterior to mid line in small specimens, anterior in larger ones (ratio posterior umbonal to total length 0.39 in specimen 0.66 mm and 0.56 in specimen 2.84 mm), low in profile, medially directed; dorsal shell margins slope gently from umbos, anterior dorsal margin short, proximally slopes gradually then somewhat angular to curve of anterior margin, thus the anterior margin does not form a smooth curve, but ventrally forms part of evenly curved ventral margin, posterior dorsal margin curves gradually to point approximately level with second distal tooth then angles and forms convex dorsal edge of rostrum, ventral margin sinuous marking ventral limit of rostrum; moderate keel from umbo to tip of rostrum, concentric ridges curve through 90° over keel; hinge plate moderately broad, anterior

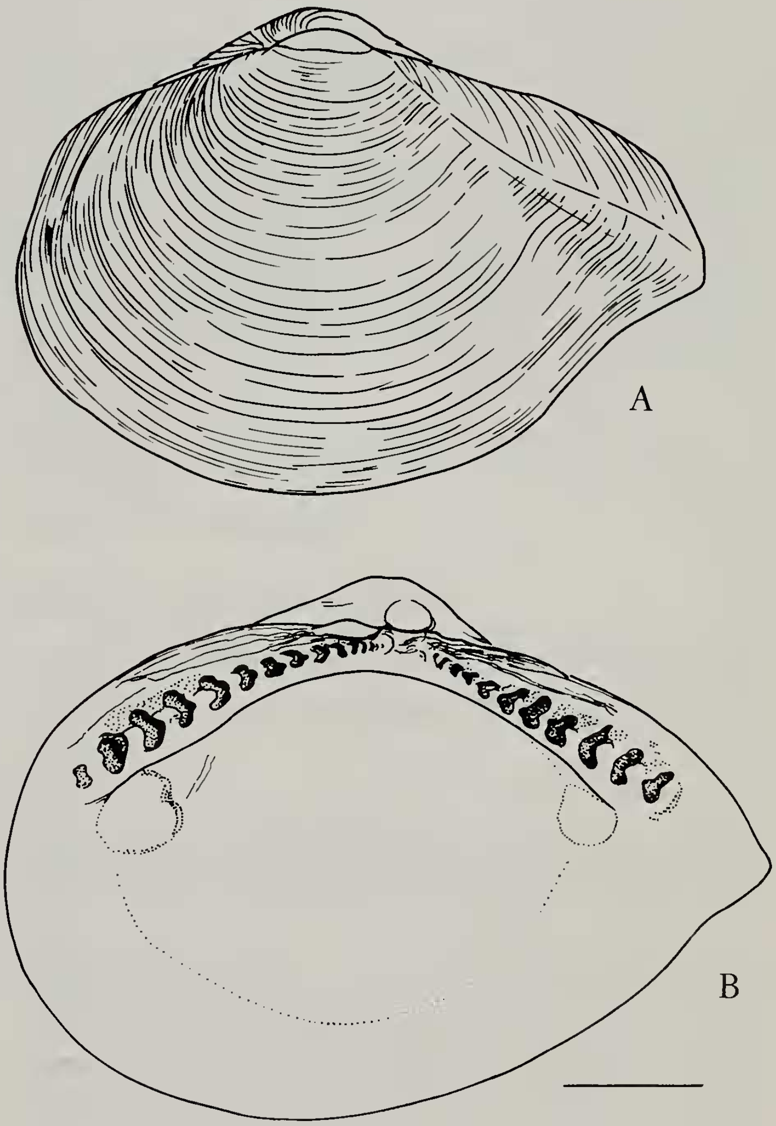

Fig. 30 *Ledella jamesi*: (a) Left lateral external view of the shell from Station 301; (b) Internal lateral view of right valve from Station 301. (Scale = 1 mm).

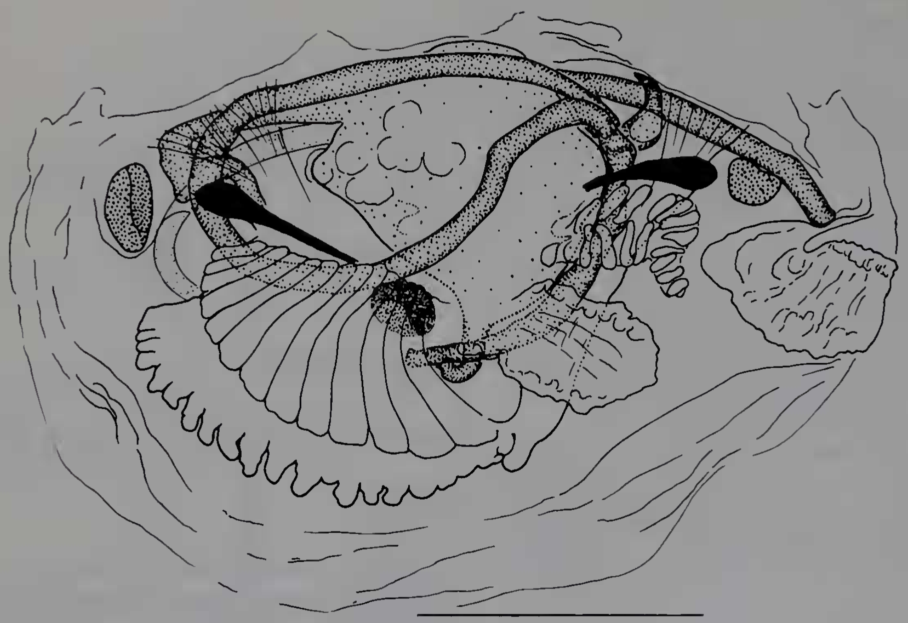

Fig. 31 *Ledella jamesi*: Lateral view of specimen from the left side with shell removed to show arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 5.

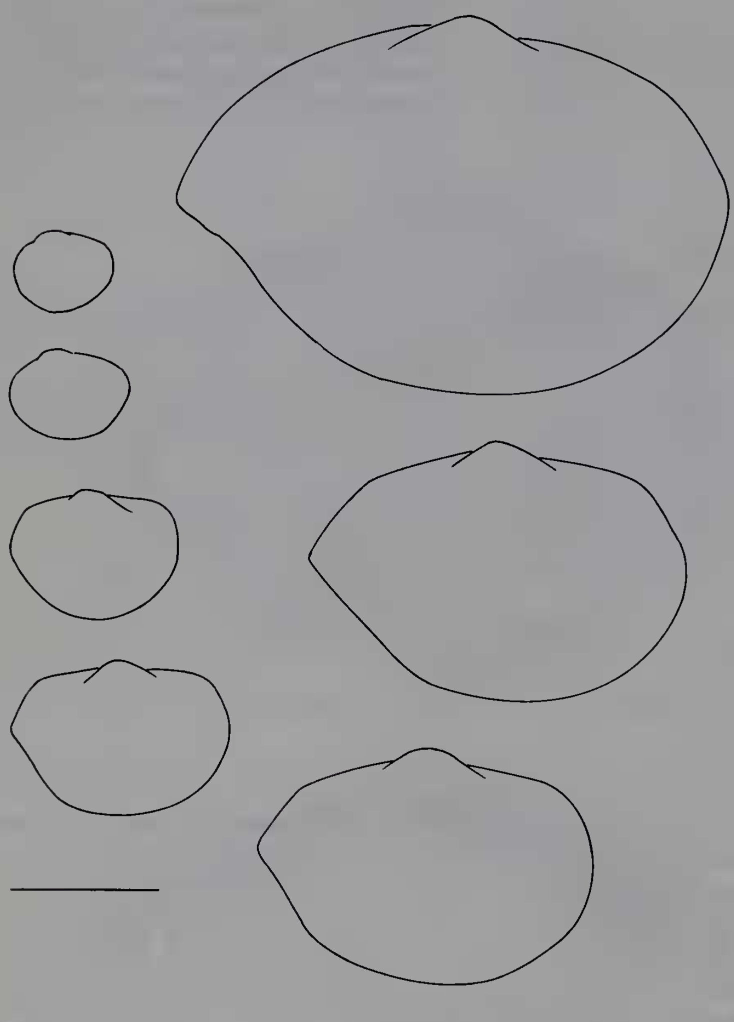

Fig. 32 *Ledella jamesi*: Growth series of shells from Station 239 in lateral outline to show change with increasing size. (Scale = 1 mm).

and posterior parts with 7–11 strong chevron teeth, the number varying with size of shell; ligament amphidetic, inner part approximately rectangular in shape, external part extending very short distance on either side of umbos; internally shell white and glossy, adductor scars and pallial line visible externally; periostracum cream with 'tortoise shell' pattern effect in some specimens.

Larval shell length 150 μm, maximum shell length 5.48 mm.

INTERNAL MORPHOLOGY. The basic form of the body is similar to *L. pustulosa* (Figs. 11 & 31). The middle and inner folds of the mantle are relatively well devloped. The anterior sense organ lies far forward, anterior to the anterior adductor muscle. The adductor muscles are relatively small, the anterior being larger than the posterior. The combined siphon is deep, but the musculature is less well developed than that in *L. pustulosa*. In most specimens the siphonal tentacle is on the right side.

The gills are moderate in size with approximately 14 plates to each demibranch. Posteriorly the inner demibranchs lie close together beside the internal edge of the siphon. In some sections the frontal cilia appear to interlock and possibly, in part, function to guide the faecal rods to the siphon. The palps are large with 14–20 ridges, the number varying with the size of the individual. The palp proboscides are also relatively large.

The foot is well developed and anteriorly directed. A small 'byssal' gland lies at the junction of the well developed heel region from the rest of the foot. The foot has many fringing papillae which are particularly long and conspicuous in this species. The form suggests a particularly active mode of life. Possibly correlated with this is a well developed nervous system. The cerebral, visceral, and pedal ganglia are particularly large, the cerebral and visceral being elongate and the joining commissures being particularly stout.

The digestive tract is similar to that in *L. pustulosa*. There is a large stomach with 6–7 sorting ridges externally visible. The style sac penetrates deep into the foot. The hind gut, which can be seen through the shell, forms two loops, one on each side of the body. As in *L. pustulosa* (Fig. 11) the course of the hind gut is somewhat variable with one or both loops either deformed or abnormally twisted.

Developing gonads were observed in animals greater than 2.0 mm in length. Approximately equal numbers of males and females were recorded. In sections the percentage of the body space filled by the testis increased from about 14.5% in a specimen 2.0 mm in length to 40% in a specimen 3.7 mm in length. In even larger animals this percentage decreased, for example approximately 26% of the body space was occupied by testis in an individual 4.3 mm in length. From sections, a female 2.3 mm in length, contained 28 ova with a maximum length of 85 μm, while another, 3.3 mm in length, contained

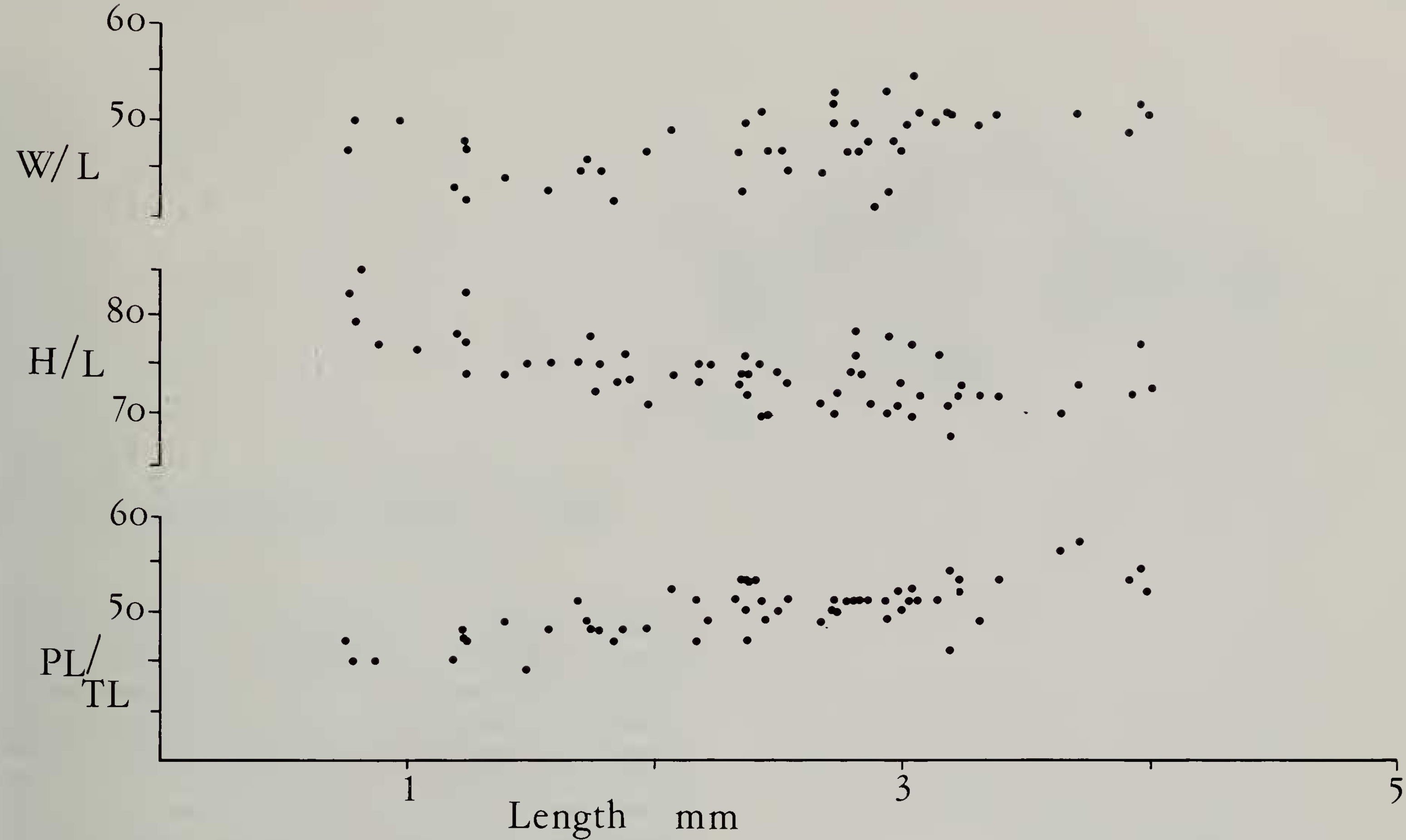

Fig. 33 *Ledella jamesi*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 239.

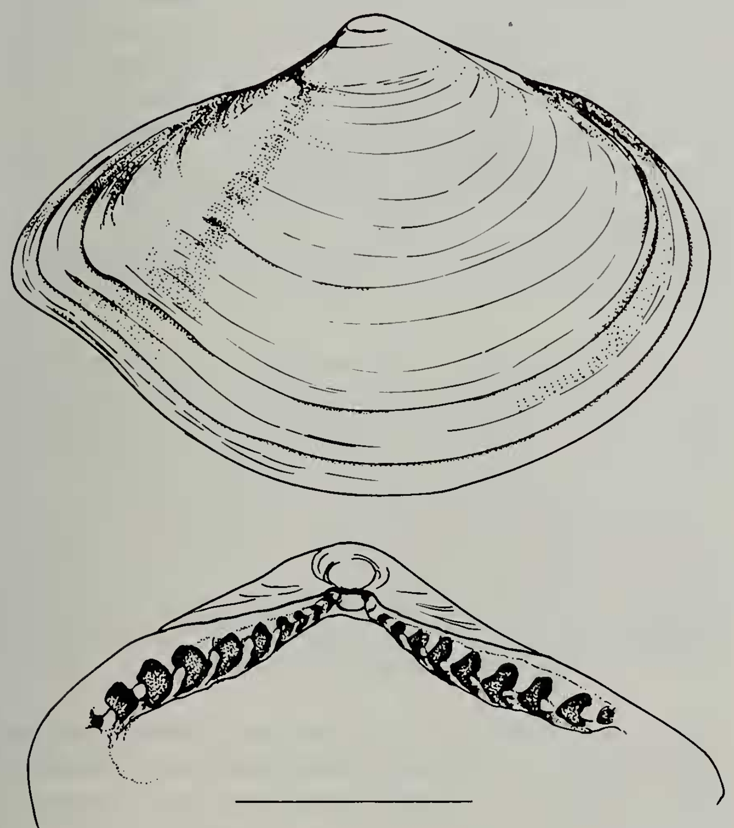

Fig. 34 *Ledella lusitanensis*: Right lateral external view of shell from Station 142 and internal view of hinge region of right valve from Station 142. (Scale = 1 mm).

219 ova with a maximum length 150 μm. Most ova were found posterior to the stomach.

In the course of growth, the rostrum becomes more pronounced with a gradual shift in the umbo-rostral length to total length ratio with increasing length. At the same time there is an overall decrease in the height/length ratio but in the width/length ratio changes little. The curvature of the dorsal margin also changes with age (Figs. 32 & 33). In young specimens it is distally straight and proximally angulate before curving to the anterior and posterior margins but with increasing age the dorsal margin becomes convex and with a more gradual curvature.

Distribution. South and West Atlantic, Argentine and Surinam Basins and Gulf of Mexico.

Depth range. 1456–2853 m.

Ledella lusitanensis new species

Holotype. BM(NH) 1988088; 2 Paratypes: BM(NH) 1988089

Type locality. Atlantis II Station 142, 10°30′N 17°51′W.

Material.

Cruise	Stn	Depth(m)	No	Lat	Long	Gear	Date
			WEST EUROPEAN BASIN				
Jean Charcot (Biogas VI)	CP24	1995	2	44°08.1′N	4°16.2′W	CP	31.10.74
			CAPE VERDE BASIN				
Atlantis II	142	1624–1796	28	10°30.0′N	17°51.5′W	ES	5. 2.67
31	147	2934	18	10°38.0′N	17°52.0′W	ES	6. 2.67
			ANGOLA BASIN				
Atlantis II 42	194	2864	1	22°54.0′S	11°55.0′E	ES	17. 5.68

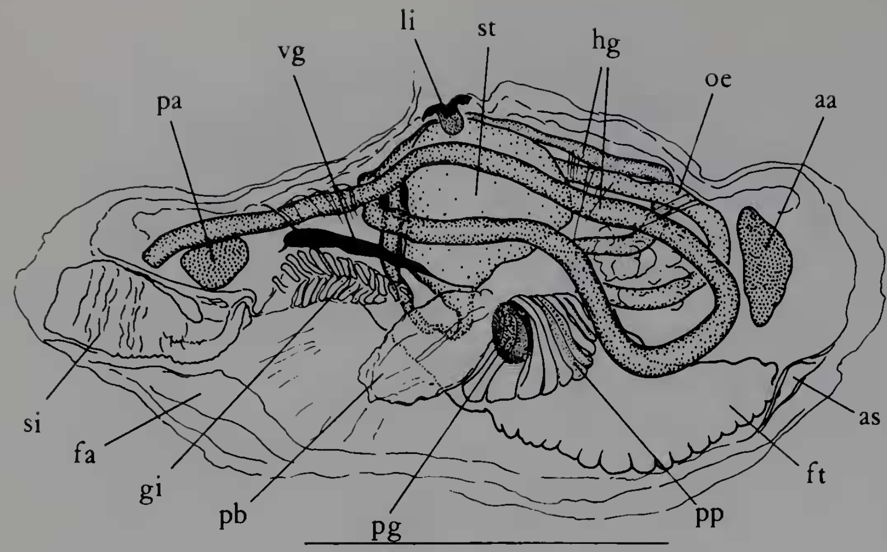

Fig. 35 *Ledella lusitanensis*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm).

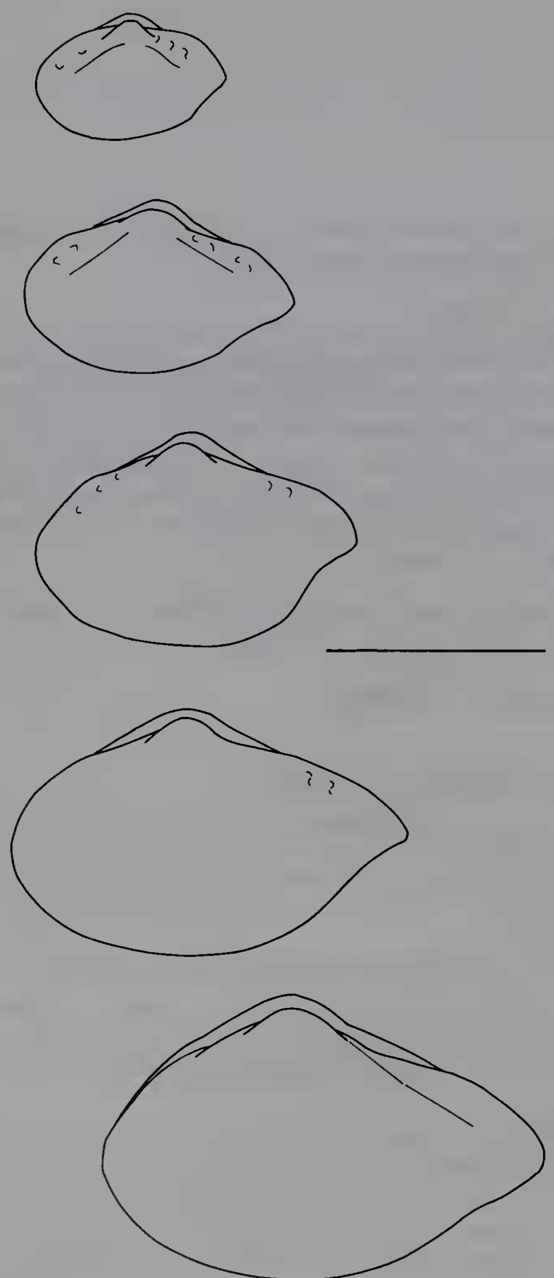

Fig. 36 *Ledella lusitanensis*: Growth series of shells from Station 142 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

DESCRIPTION (Fig. 34). Shell moderately strong, inflated, almost equilateral, rostrum long, pointed; umbos slightly anterior in position, raised, posteriorly directed; shell ornamented with fine concentric ridges with superimposed pattern of light and darker bands of variable width; dorsal margin moderately convex, antero-dorsal margin slopes from umbo to anterior limit of hinge plate, then curves evenly to form rounded anterior margin, postero-dorsal margin proximally slopes gently, distally more acutely to form rostrum, posterior ventral margin not markedly sinuous, ventral margin long, smooth, moderately convex, moderate keel from umbo to point of rostrum; hinge plate very broad, strong, relatively long, anterior and posterior parts each with approximately 10 chevron teeth (number depending on size of animal), distal teeth extremely strong, well developed, proximal teeth progressively smaller, those bordering internal ligament small and rudimentary; ligament amphidetic, internal part rectangular, short external extensions, equal in length, on either side of umbos.

Larval shell length 190 μm; maximum recorded shell length 3.85 mm.

MORPHOLOGY. Although the form of the body and mantle is similar to that of other species, the foot of *Ledella lusitanensis* is distinctive in being long, slender and having a more anteriorly directed attitude than that of other species described here (Fig. 35). The species is likely to have a very active mode of life. The foot itself is extremely muscular and the retractor muscles being particularly well developed. Correlated with this is a large oblong-shaped pedal ganglion, with other parts of the nervous system being generally well developed. A large byssal gland is present in the heel of the foot.

The siphon although poorly preserved in several preparations, is similar in structure to that described for *Ledella pustulosa* with large haemocoelic spaces between the muscle fibres. Considerable quantities of faecal material were found between the inner muscular lobes of the well developed feeding aperture but this is likely to have been an effect from the sample collection and processing. The siphonal tentacle is to the right side of the extreme inner limit of the siphonal embayment.

The gills are of moderate size with approximately 14 gill plates. The palps are similar to those of *Ledella sublevis* with 10–12 ridges. The stomach is large and well developed with

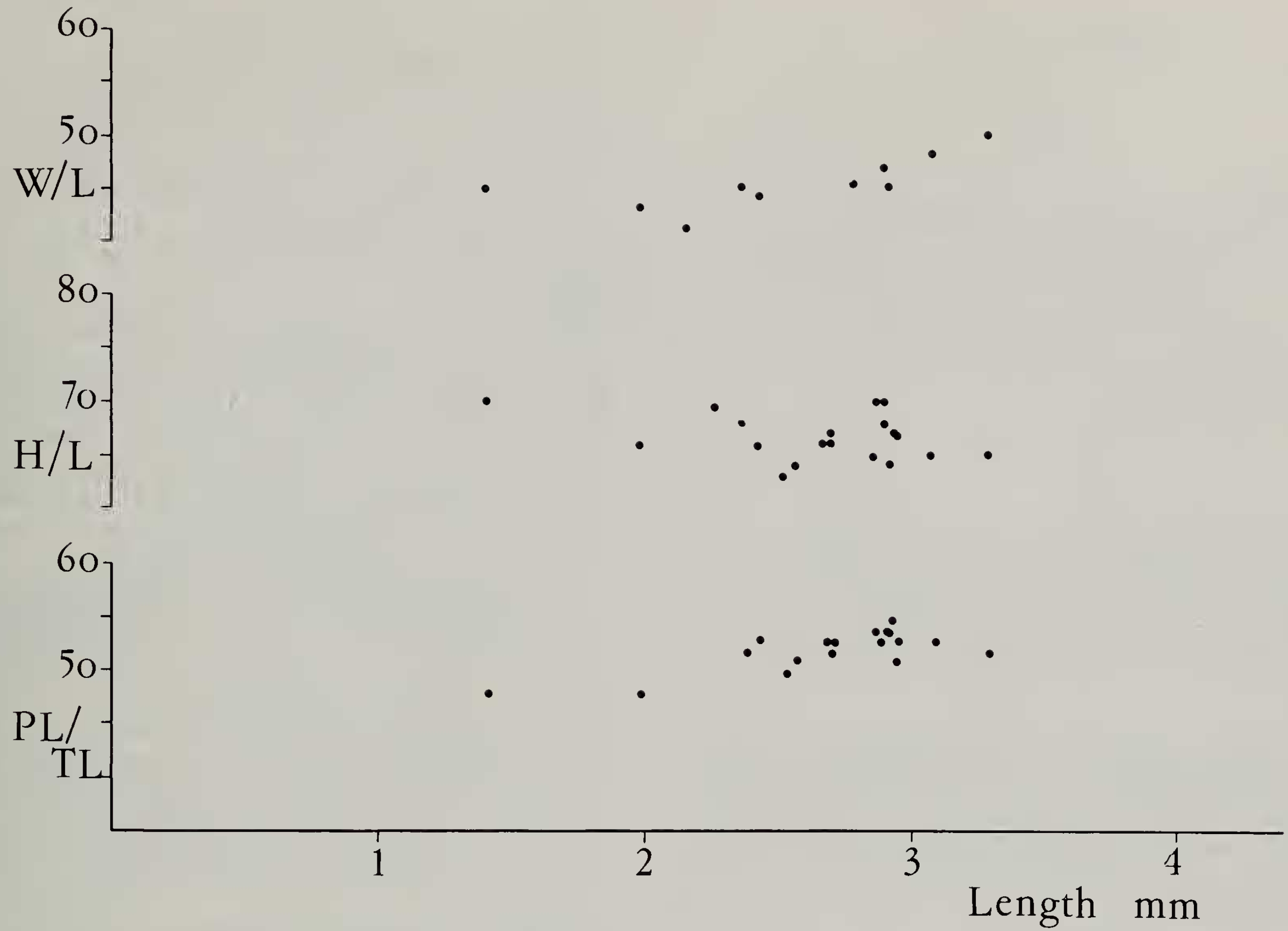

Fig. 37 *Ledella lusitanensis*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 142.

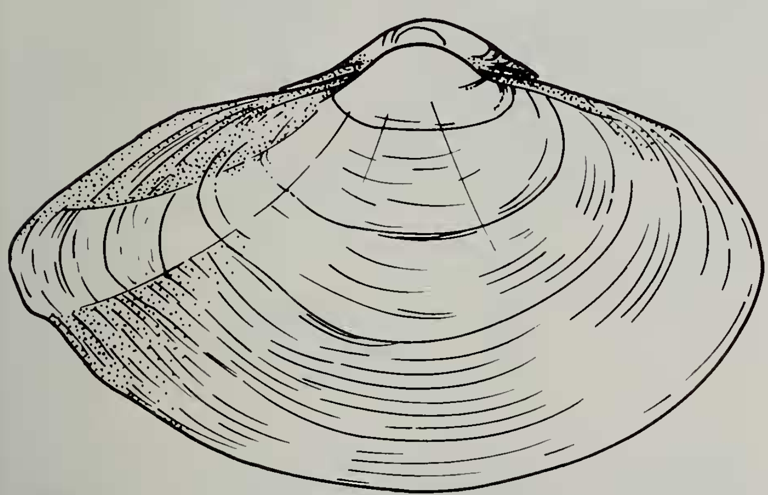

Fig. 38 *Ledella sandersi*: Right lateral external view of the shell from Station 191. (Scale = 1 mm).

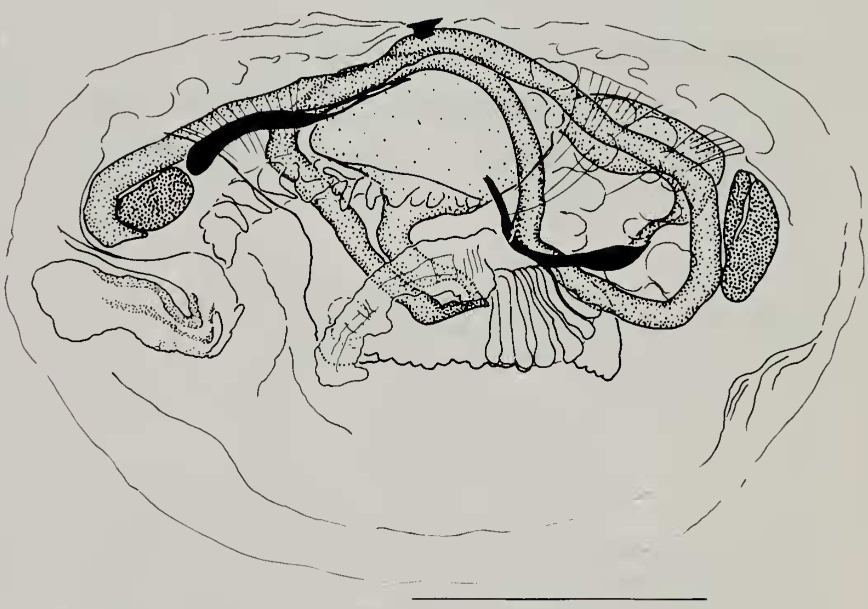

Fig. 39 *Ledella sandersi*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 0.5 mm). For identification of parts see Fig. 35.

the openings to the left digestive diverticula dorsally on the left wall. One is immediately posterior and ventral to the oesophagus, the second is at approximately the same level and ventral to the tooth of the gastric shield. The shield is well developed. The style sac penetrates the upper half of between 1/3 – 1/2 of the ventral distance of the foot. The hind gut forms a single loop to each side of the body, the shape of the loops being similar to that of the right loop of *Ledella modesta*. The cross over point lies a short distance posterior to the ligament rather than immediately so as in *L. pustulosa*.

Few specimens of this species were intact and only two could be sectioned. Both were male, in the smallest (2.4 mm) the testis was slightly developed (2% of body area) while in the larger (3.1 mm) 16% of body area was covered by testis.

In the course of growth, the rostrum becomes more elongate with a slight shift in the total length/umbo-rostral length ratio (Figs. 36 & 37) and the dorsal margin becomes less convex. There is little change in the height/length and the width/length ratios.

This species is somewhat similar in appearance to *L. sublevis* but the shell is slightly smoother, more elongate and

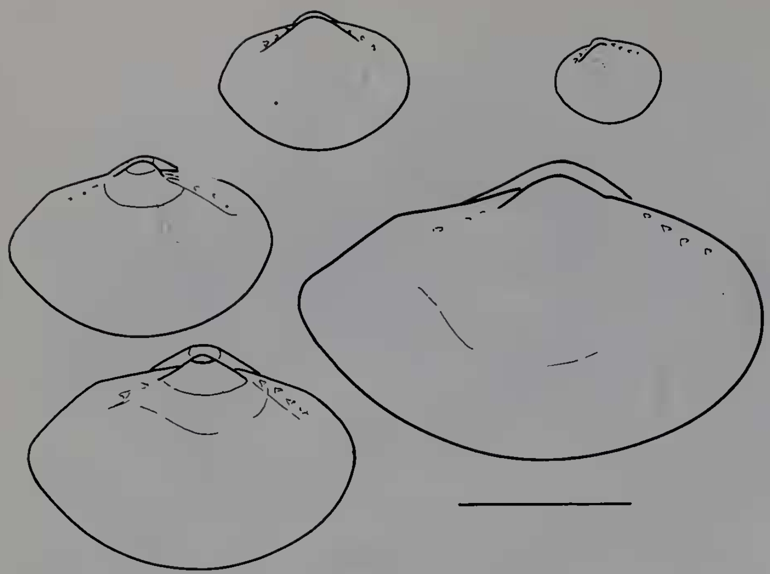

Fig. 40 *Ledella sandersi*: Growth series of shells from Station 191 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

the rostrum more pointed. The hinge plate and number of teeth are similar in the two species but *L. lusitanensis* has a stronger hinge and the lower edge of the hinge plate curves more sharply towards the internal ligament. When the population variations in *L. sublevis* are taken into account this difference is less obvious.

DISTRIBUTION. Eastern Atlantic.

DEPTH RANGE. 1624–1995 m.

Ledella sandersi new species

HOLOTYPE. BM(NH) 1988090; 5 Paratypes: BM(NH) 1988091

TYPE LOCALITY. Atlantis II Sta. 191, 23°05′S, 12°31.5′E, 1546–1559 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			ANGOLA BASIN				
Atlantis II	191	2546–2559	14	23°05′S	12°31.5′E	ES	17. 5.68
42	192	2117–2154	2	23°02′S	12°19.0′E	ES	17. 5.68
	194	2864	1	22°54′S	11°55′E	ES	17. 5.68

This species is very closely related to *L. verdiensis* (p. 000). The main differences are that the shell is smaller, wider and deeper, with the umbo slightly more central in position. The gills and palps are longer and larger and the foot is small.

DESCRIPTION (Figs 38 & 40). Shell moderately elongate, equilateral or almost so, rostrum blunt, fine concentric sculpture; umbos large, raised, directed medially; antero-dorsal margin straight or almost so, slopes gently to anterior limit of hinge plate where it makes a small angle with rounded anterior margin, postero-dorsal margin also straight or almost so, slopes gently to posterior limit of hinge plate where it makes a marked angle with dorsal margin of rostrum, the edge of which is also straight or almost so, posterior ventral margin not sinuous except in larger specimens which are faintly sinuous, broad, oblique, somewhat raised rostral ridge, shell margin anterior and posterior to umbos raised and slightly sulcate at base of raised part; anterior and posterior hinge plates angular, distally broad but narrow below umbos with relatively few, broad, chevron-shaped teeth, 6 or 7 on each plate; ligament internal, amphidetic, with a small, narrow posterior external part.

Larval shell length 265–285 µm, maximum recorded shell length 3.96 mm.

MORPHOLOGY. The morphology is very similar to *L. verdiensis* and differs only in the relative size of the various organs (Fig. 39). The adductor muscles are large and oval, the anterior slightly larger than the posterior and the inner mantle fold is broad with well developed musculature. The combined siphons are broad and elongate but the ventral margin is not fused nor the junction between the inhalent and exhalent part.

The gills are relatively long extending half across the body, individual gill plates are thick and are approximately 12 in number. The palps are small with approximately 9 folds, the palp proboscides are elongate and narrow. The foot is small and relatively short. The mouth is set far posterior to the anterior adductor muscle, with the oesophagus forming an anteriorly directed semicircle before joining the large stomach. The hind gut makes a single loop to the right side of the body. The visceral and cerebral ganglia are both stout and cylindrical.

DISTRIBUTION. Lower slope depths off Angola.

DEPTH RANGE. 1546–2154 m.

Ledella similis new species

HOLOTYPE. BM(NH) 1988092

TYPE LOCALITY. Sarsia Sta. 63, 46°17.5′N, 4°45.2′W, 1336 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			WEST EUROPEAN BASIN				
Sarsia	S.63	1336	8	46°17.5′N	4°45.2′W	ED	24. 7.67

Although the umbos are larger, this species, at first sight, and in external view can be mistaken for *Ledella oxira* (p. 148) or *Ledella parva* (p. 165), however there is a marked difference in hind gut configuration and there are fewer hinge teeth.

DESCRIPTION (Figs 41a, b & c). Shell inequilateral, laterally compressed, elongate-oval in outline with small, blunt posterior rostrum, pattern of light and dark banding, ornament very fine lines of growth; umbos posterior, raised, posteriorly directed; dorsal margin convex, elongate antero-dorsal margin curves almost evenly to narrow anterior margin, postero-dorsal margin slopes first gradually then more steeply to form the dorsal margin of the rostrum, posterior ventral margin with short sinuosity, ventral margin moderately convex; inconspicuous ridge from umbo to tip of rostrum; anterior hinge plate moderately long, broad distally, narrow below umbo, with relatively straight ventral edge, 10 teeth, proximal teeth very small, posterior hinge plate short, ventral edge

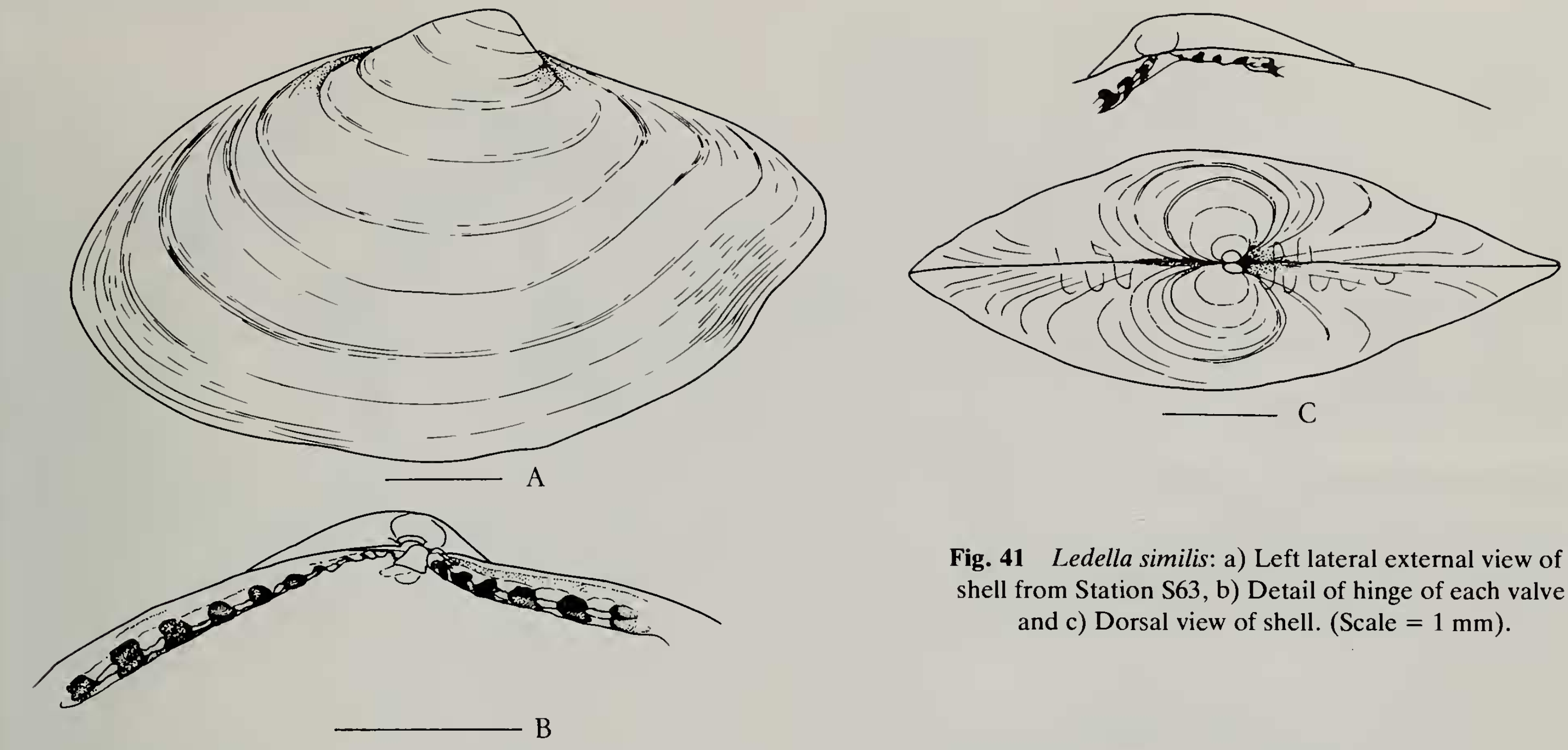

Fig. 41 *Ledella similis*: a) Left lateral external view of a shell from Station S63, b) Detail of hinge of each valve; and c) Dorsal view of shell. (Scale = 1 mm).

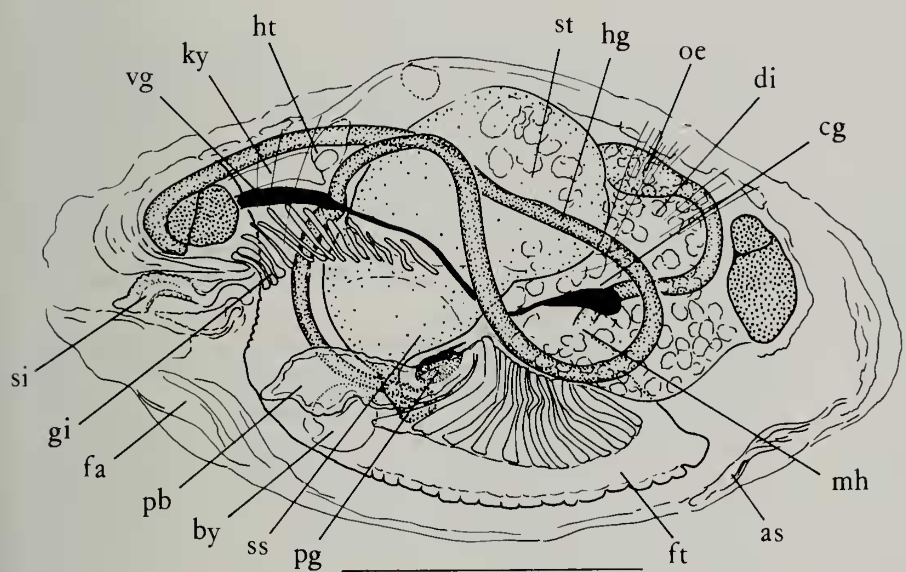

Fig. 42 *Ledella similis*: Lateral view of specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm).

curved, relatively few (6–7) broad chevron-shaped teeth; ligament amphidetic, short, extending below hinge plate with external part consisting of small narrow section posterior to umbo and longer section anterior to umbo.

Larval shell length 210 µm, maximum recorded shell length 6.08 mm.

MEASUREMENTS. Because of the limited number of animals available, shell measurements (mm) were limited to two intact specimens and one opened specimen:-

Length	Height	Width	H/L	W/L	P/Umbo/Total	Teeth (Ant/Post)
4.78	2.91	1.70	0.61	0.34	0.45	
6.08	3.57	2.21	0.59	0.36	0.48	
4.02	2.42		0.60		0.43	10/7

Internal Morphology:
Of the eight specimens, three were decalcified and stained as whole mounts (Fig. 42). The mantle differs little from those species already described. A pair of lateral central ridges between inhalent and exhalent parts of the siphon may function to separate the exhalent and inhalent currents. The tentacle arises from a shallow pocket on either the left or right side at the base of the siphonal embayment. The feeding aperture is well developed, as is the anterior sense organ ventral to the anterior adductor muscle. The adductor muscles differ in size; the anterior being the larger and crescent-shaped. The posterior muscle is more rounded.

The foot is large, with a large, spherical 'byssal' gland and a small posteriorly extended heel. The gills are well developed with approximately 23 filaments. The labial palps are moderately large with 11 broad ridges. The palp proboscides are large and much folded in the contracted state.

The mouth is not far removed from the anterior adductor muscle. The stomach and style sac are large and lie diagonally within the body, the latter penetrating deep into the foot. From the style sac the course of the hind gut is just ventral to the pedal ganglia and then parallels the style sac, posterior to the stomach to the dorsal margin from where it forms a single loop on the right side of the body, which lies short of the anterior adductor muscle. The cerebral ganglia are relatively small, while the pedal ganglia lie central in the foot.

Although the three stained specimens, measure between 4.02–6.08 mm in length (making this one of the larger species of *Ledella*), there were no signs of gonads.

DISTRIBUTION. Bay of Biscay, 1336 m.

Ledella verdiensis (new species)

HOLOTYPE. BM(NH) 1988093

TYPE LOCALITY. Discovery Sta. 8528 No. 1, 17°38′N, 18°35′W, 3150–3155 m.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			CAPE VERDE BASIN				
Discovery	8528	3150–3155	9	17°38′N	18°35′W	WS	2. 7.74

DESCRIPTION (Fig. 43). Shell, inequilateral, elongate oval, rostrate, moderately compressed, strong concentric ridges becoming wider ventrally; umbos large, raised, anterior to midline, directed medially; antero-dorsal margin moderately convex, slopes to form continuous curve with anterior and the ventral margin, postero-dorsal proximal margin straight, moderate slope to posterior limit of hinge plate where it makes an angle to dorsal margin of rostrum, postero-ventral margin very slightly sinuous; anterior and posterior hinge plates elongate, distally broad, proximally narrow below umbo, teeth stout, broad, chevron-shaped 10–12 in anterior series, 8–10 in posterior, number depending on size of shell; ligament internal, amphidetic, triangular, relatively small; pallial sinus deep.

Larval shell length 295 μm, maximum recorded shell length 4.74 mm.

As the size of the shell increases so, to some degree, does the proportionate length of the rostrum compared with total length, consequently there is a small, relative, anterior shift in the position of the umbos.

MORPHOLOGY. The morphology is similar to other species described above (Fig. 44). The adductor muscles are approximately equal in size and oval in cross section. There is a minimal amount of mantle fusion. The siphon is not fused along its ventral margin, nor is it formed into separate inhalent and exhalent parts. However, there is an internal lateral median, longitudinal siphonal ridge on each side, which in life probably separates the inhalent and exhalent parts as well as acting as a guide during the voiding of the faecal rods. There is also a well developed feeding aperture similar to that described for *L. pustulosa* formed by the extension and apposition of the inner and outer mantle lobes. A siphonal tentacle is attached on the right side in the depth of the siphonal embayment. The anterior sense organ is well developed and far anterior in position.

Fig. 43 *Ledella verdiensis*: Left lateral external view of a shell from Discovery Station 8528 and detail of hinge plate of the right valve. (Scale = 1 mm).

The gill axis is relatively short and for the most part lies posterior to the body. The gill plates are small and number 14–16. The palps are very small with few ridges but an extremely long thin palp proboscis is present. The foot is elongate, slender and anteriorly directed, the halves of the divided sole are slender. The 'byssal' gland is small while the pedal ganglia are large, elongate and each with a well developed statocyst dorsal to it. The visceral and cerebral ganglia are moderately large.

The mouth is situated somewhat posterior to the anterior adductor muscle. The wide oesophagus enters high on the anterior dorsal face of the large stomach. The style sac is short. The hind gut, after penetrating deep into the foot, forms one loop on the right side of the body. The digestive diverticula lie for the most part anterior to the stomach, with one portion to the right and a larger portion to the left of the body. Part of the latter differs in appearance from the remainder, the tubules being somewhat larger and slightly lighter in colour compared with the others. This distinction has been observed in other nuculanids (p. 129) and probably reflects a division of function. Differences similar to those described for *N. minuta*, occur in the digestive ducts that serve the three portions of the digestive diverticula. The kidney is somewhat enlarged and extends anteriorly into the body to the right side of the stomach.

DISTRIBUTION. Abyssal depths off the Cape Verde Islands, 3150–3155 m.

Ledella oxira (Dall, 1927)

HOLOTYPE. USNM No. 108190.

TYPE LOCALITY. Off Southeast coast of United States (Lat. 30°58′N, Long. 79°38′W), 678 m.

SYNONYMY. *Leda oxira* Dall 1927 *Proc. U.S. natn. Acad. 70*, art. 18, p. 8, 9.
Ledella oxira Johnson 1934 *Proc. Boston Soc. 40*, p. 16.

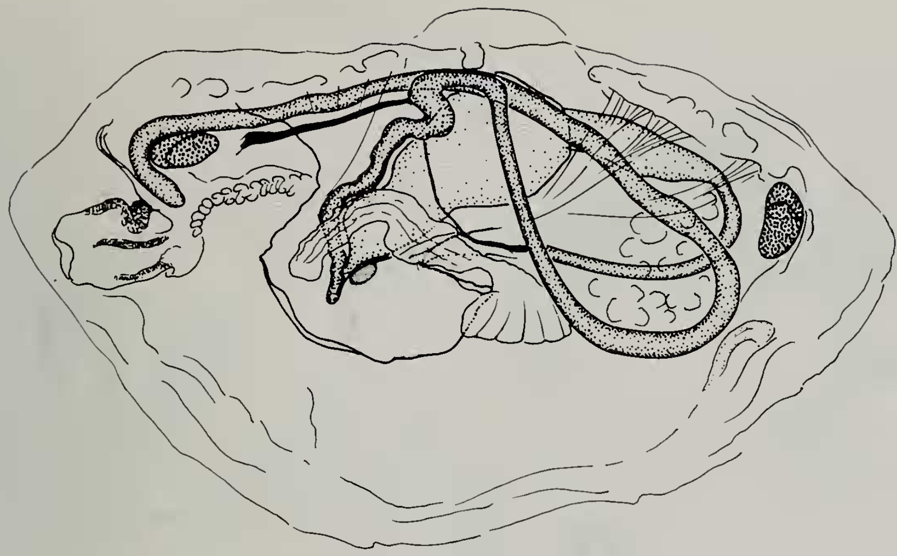

Fig. 44 *Ledella verdiensis*: Lateral view of a specimen from the right side with the shell removed to show the arrangement of the body organs. (Scale = 1 mm). For identification of parts see Fig. 42.

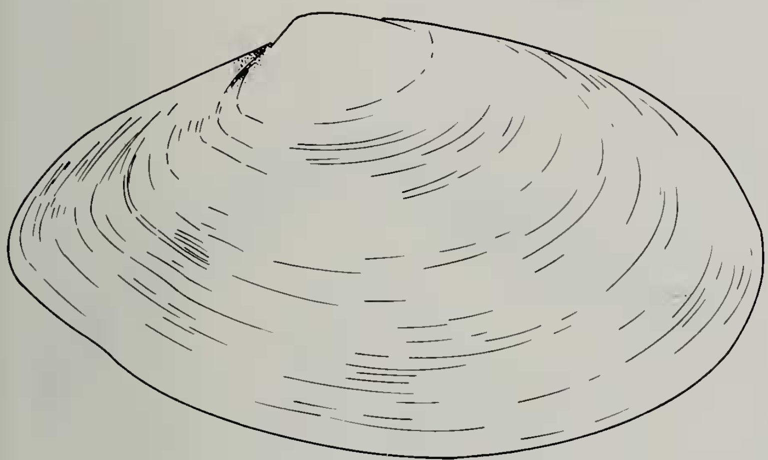

Fig. 45 *Ledella oxira*: Right lateral external view of shell from Station 167. (Scale = 1 mm).

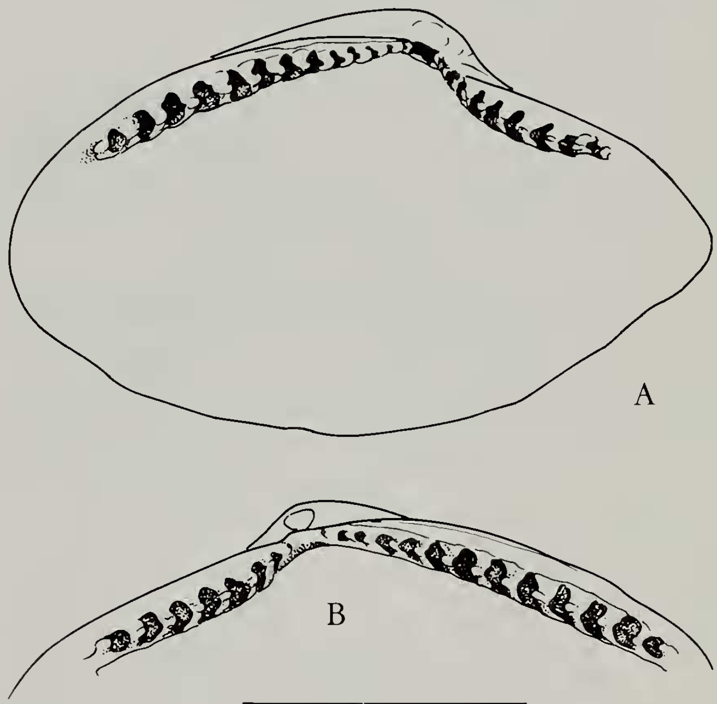

Fig. 46 *Ledella oxira*: (a) Lateral internal view of right valve of the holotype specimen (USNM No. 108190); (b) hinge plate detail of left valve from Station 167. (Scale = 1 mm).

MATERIAL. USNM No. 108190.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
				BRAZIL BASIN			
Atlantis II 31	162	1493	1	8°02.0′S −7°56.0′S	34°03.0′W −34°09.0′W	ES	19. 2.67
	167	943–1007	2	7°58.0′S −7°50.0′S	34°17.0′W	ES	20. 2.67

This species resembles both *Ledella parva* and *Ledella semen* in its shell characters. Nevertheless, the anatomy of *L. oxira*, and the course of the hind gut in particular, differs markedly from *L. parva*. The possible synonymy with *L. semen* is discussed later. (p. 166).

DESCRIPTION (Fig. 45 & 46a & b). Shell inequilateral, elongate-oval, laterally compressed, moderately strong, surface smooth with fine lines of growth; short, blunt umbo far posterior, slightly raised, somewhat posteriorly inclined; anterior and posterior dorsal margin moderately convex, antero-dorsal margin forms long smooth curve with anterior margin, short postero-dorsal margin proximally straight, or almost so, slopes gradually to posterior edge of hinge plate, thereafter more acutely to form dorsal margin of short rostrum, postero-ventral margin slightly sinuous, ventral margin long, smooth and moderately convex; small inconspicuous ridge from umbo to tip of rostrum; hinge plate moderately strong, relatively broad, narrower below umbo, anterior hinge plate long, ventral edge relatively straight, 13 teeth, posterior hinge short, ventral edge curved towards umbo, 8 teeth; ligament amphidetic, relatively elongate, does not extend ventral to hinge plate.

MEASUREMENTS (mm).

Length	Height	Width	H/L	W/L	P. umbo/TL	Teeth Ant./Post.
3.12	1.80		0.58		0.38	13/8
1.74	1.09	0.62	0.62	0.35	0.40	

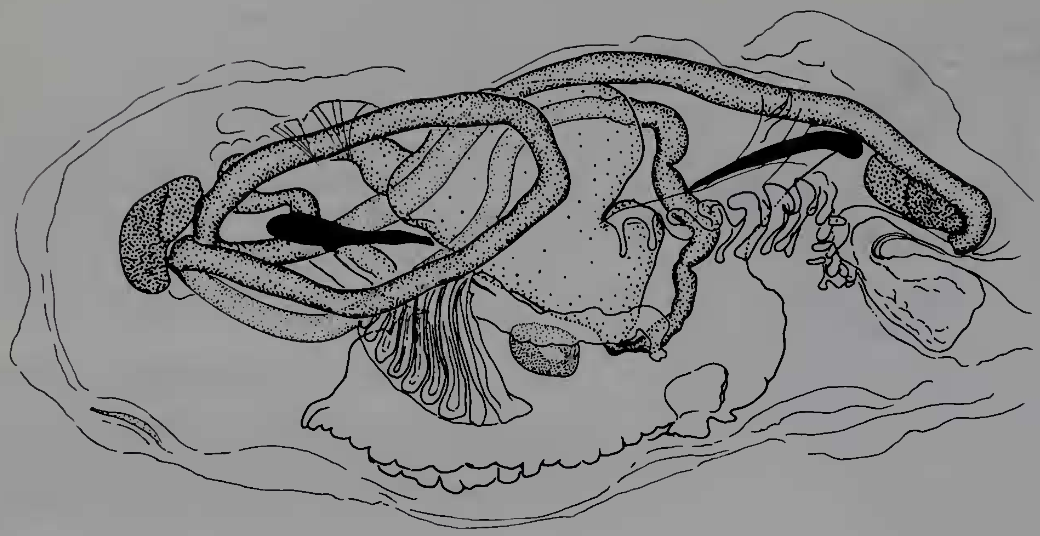

Fig. 47 *Ledella oxira*: Lateral view of a specimen from the left side with the shell removed to show the arrangement of body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

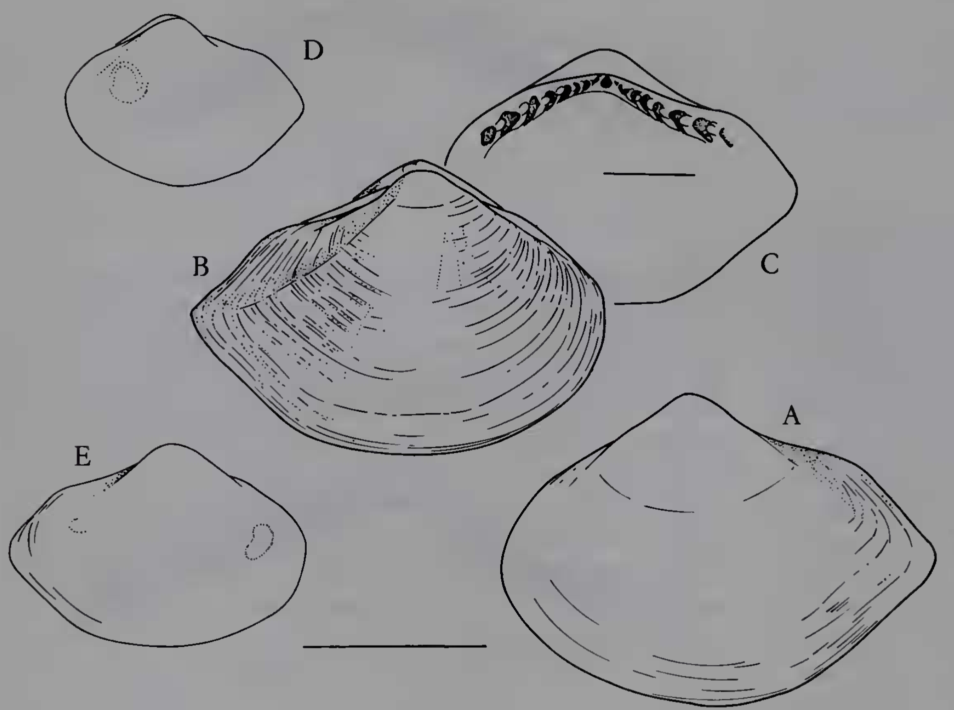

Fig. 48*Ledella galatheae*: a) Left lateral external view of holotype, b) right lateral external view of specimen from Biogas VI Station DS 78, c) right lateral internal view of specimen from Station 287, d) and e) lateral external views of shells in outline from Station 287. (Scales = 1 mm; a, b, d & e drawn to same scale).

MORPHOLOGY. As there were only three specimens available, the description of the internal morphology is based on one whole mount stained in haemotoxylin (Fig. 47).

The mantle structures differ little from those described for *L. pustulosa*. The siphonal tentacle originates on the right side close to the base of the combined siphon. The adductor muscles are approximately equal in size and oval in shape; the long axes of the muscles are parallel to the shell margins.

The foot is moderately large with a large byssal gland. The nervous system is well developed with a large pedal ganglion, situated in the anterior half of the neck of the foot. The cerebral and visceral ganglia are large and club-shaped. The gills have approximately 15 pairs of alternating plates. The palps are small with 8 broad ridges while the palp proboscides are slender although much contracted in the preserved specimens. (Fig. 47).

The stomach and style sac are relatively large. The hind gut extends only a short distance into the foot before turning dorsally, posterior to the stomach. At the posterior dorsal margin of the body its course is to the right side of the body as far as the inner face of anterior adductor muscle where it crosses to the left side to form one loop before returning to the right again at the inner face of the anterior adductor. From there its course is dorsal to the anus. This configuration is but the elongation of the single-looped primitive condition

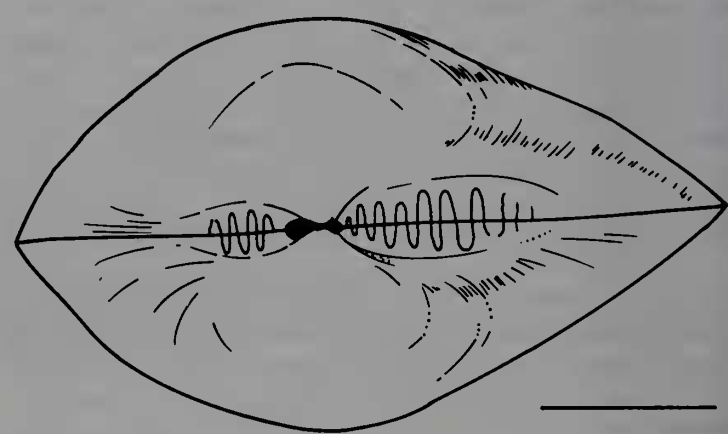

Fig. 49 *Ledella galatheae*: Dorsal view of specimen from Station 287. (Scale = 1 mm).

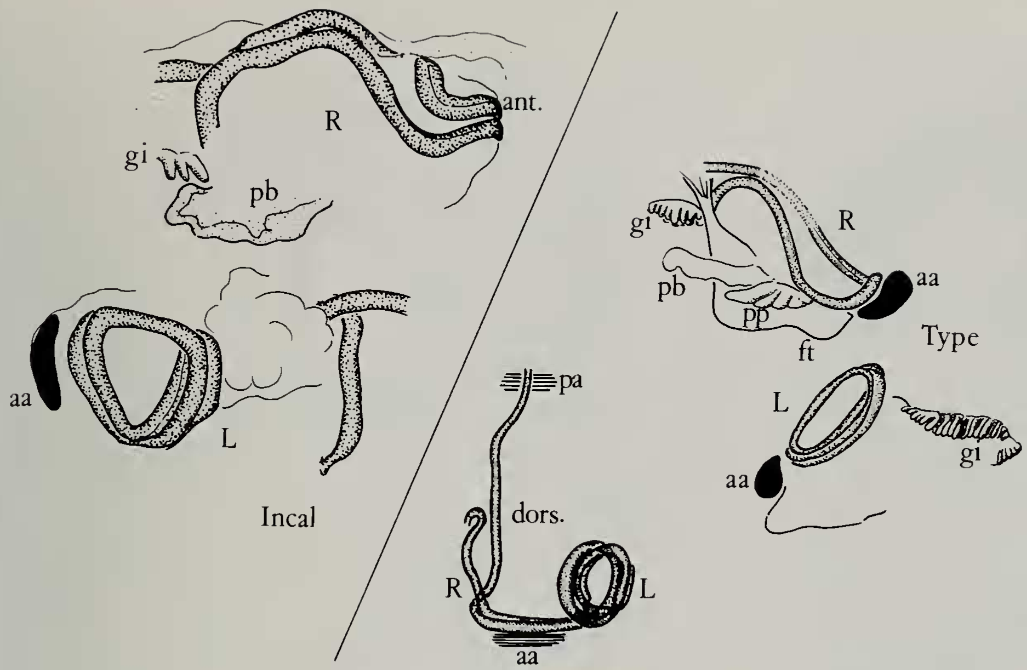

Fig. 50 *Ledella galatheae*: Comparative views of the hind gut of the type specimen (A) and the specimen from Station Incal WS03 (B).

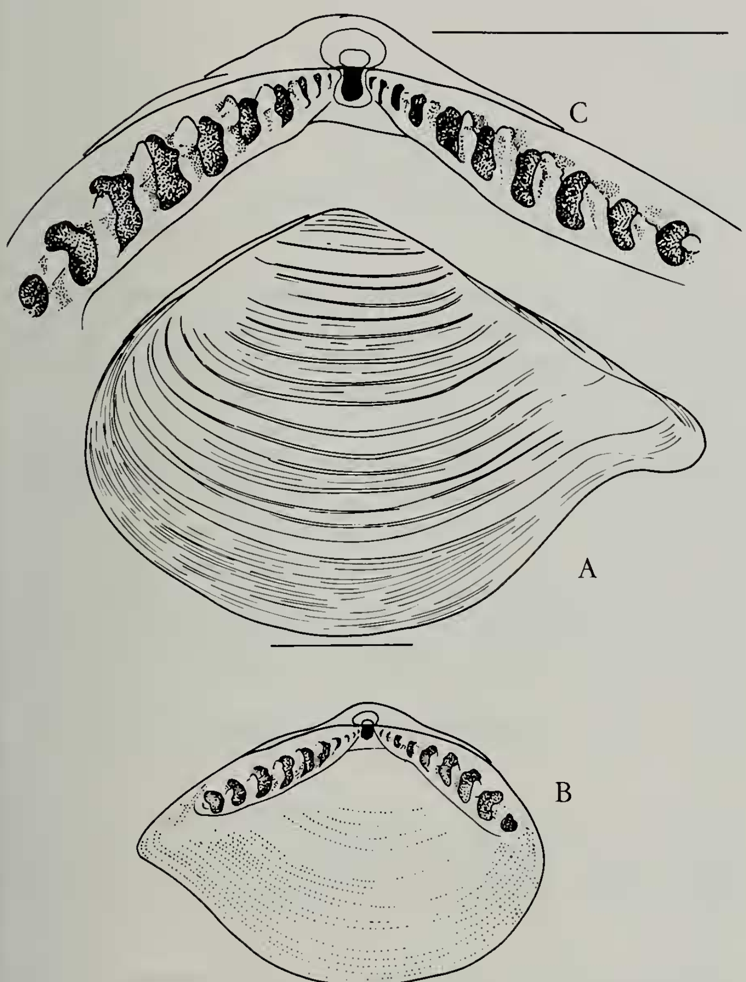

Fig. 51 *Ledella solidula*: (a) Left lateral external view of a specimen from Station 293. Note this is a large specimen with a thickened and internal ventral margin and therefore somewhat atypical (see Fig. 55); (b) left lateral internal view of a specimen from Station 118; (c) hinge of latter specimen in greater detail. (Scale = 1 mm).

which, by virtue of the space between adductor and mouth and oesophagus is able to extend to the left side of the body. Although this is a way of accommodating the lengthened hind gut it is not a common condition in deep sea protobranchs and it has been only recorded in a few other deep-sea species, notably *Yoldiella curta* Verrill & Bush (Allen, Hannah & Sanders, in m/s).

Distribution. Off coast of South America and southeast coast of U.S.A, 673–1493 m.

Ledella galatheae Knudsen 1970

Holotype. ZMUC

Type locality. 'Galathea' Sta. 30, 0°42′N, 5°59′W, 5160 m, off W. Africa.

Material. Holotype specimen.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			GUINEA BASIN				
Walda	DS31	4279	1	3°17.5′N	2°01.7′W	ES	
			SIERRA LEONE BASIN				
Knorr 25	287	4934–4980	41	13°12.0′N	54°53.8′W	ES	25. 2.72
			WEST EUROPEAN BASIN				
Jean Charcot (Biogas VI)	DS78	4706	1	46°31.2′N	10°23.8′W	ES	25.10.74
	DS81	4715	1	46°28.3′N	10°24.6′W	ES	27.10.74
(Incal)	WS03	4829	1	48°19.2′N –48°19.1′N	15°23.3′W –15°22.5′W	WS	1. 8.76

Despite earlier doubts about the identity of the above specimens (see below), comparison with the original type material leaves no doubt that the specimens in our collections are *Ledella galathea*.

Description (Figs. 48 & 49). The original shell description (Knudsen, 1970) is accurate and does not require modification, however, we found ourselves at something of a loss when we compared the anatomy of the above specimens against the original description. The internal morphology of the present specimens does not even closely resemble the description given by Knudsen (1970). The original description indicates a primitive gut morphology with a single hind gut loop to the right side of the body. In addition Knudsen (1970)

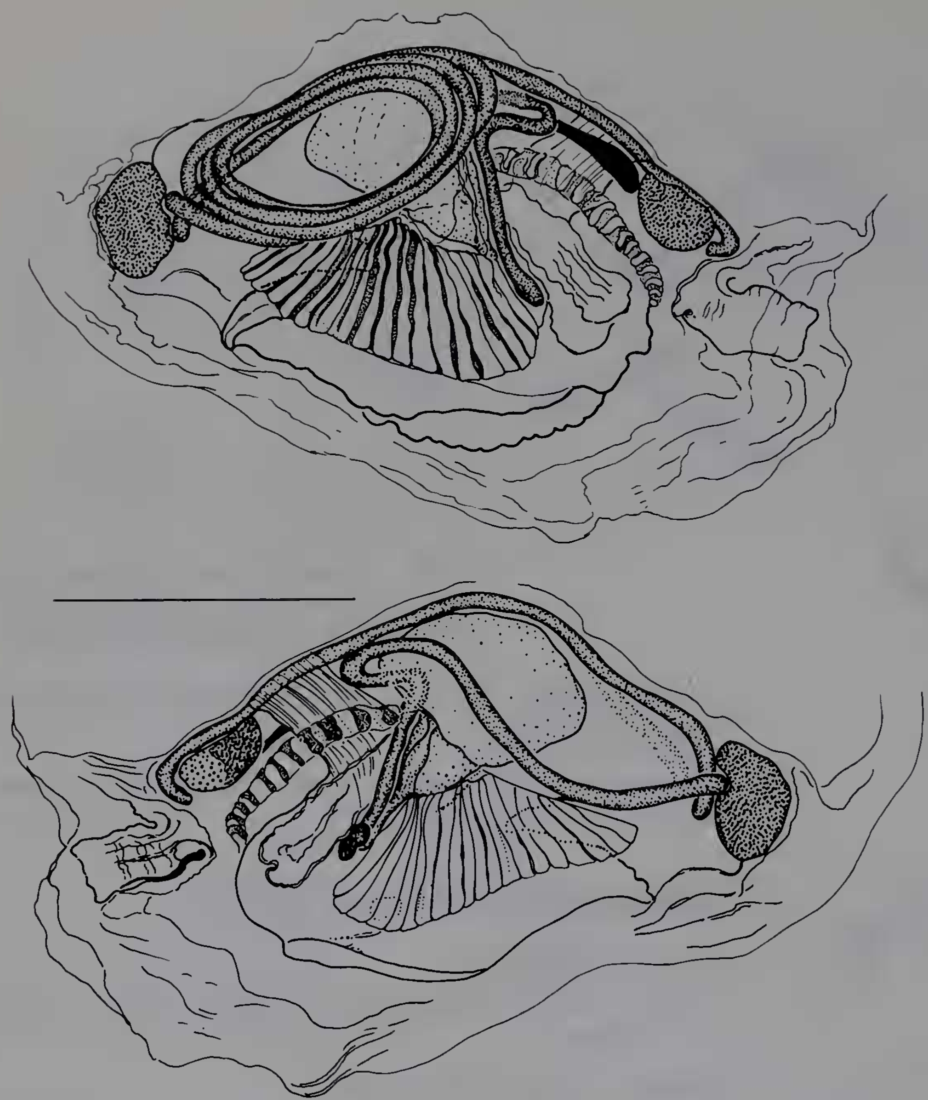

Fig. 52 *Ledella solidula*: Lateral views of a specimen from the left and right sides with shell removed to show the arrangement of the body organs. (Scale = 0.5 mm).

refers to a finely 'serrate' mantle edge at the margin of siphonal embayment. Although we have been constrained by the state of the preservation of our specimens it is clear that their morphology is similar to that of *Ledella acuminata* and *L. solidula* (Figs. 52 & 53). Thus, the hind gut passes from the right to left side of the body and forms four coils on the left side (Fig. 50). Fortunately on examination of the type specimen we found sufficient body remains to show that the anatomy of the Galathea material was the same as that of the present specimens i.e. with multiple coils on the left side. Another notable morphological character is the small size of the palp. We can only conclude that either there was an accidental transposition of a soft part drawing in the Galathea Report or that the shell relating to the body drawn by Knudsen 1970 (his figure 14c & d) was not an example of this species. This would not be at all surprising to us considering the great difficulties there are in distinguishing the younger specimens of the less common species of the subfamily from each other.

Ledella solidula (Smith 1885)

HOLOTYPE. BM(NH) 1887.2.9.2940.

TYPE LOCATION. Station 120, Challenger Expedition, off Pernambuco, 1234 m.

SYNONYMY. *Leda solidula* Smith 1885 *Chall. Rep. Lam.* p. 233, pl. 19, Fig. 6, 6a.

Nucula solidula (Smith): Aquayo & Jaume, 1950. *Catalogo Muluscos de Cuba, III, Scaphopoda, Pelecypoda*, p. 644.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
			NORTH AMERICA BASIN				
Atlantis II 24	118	1537–1830	184+ 247V	32°19.4′N –32°19.0′N	64°34.9′W –64°34.8′W	ES	18. 9.66
			GUIANA BASIN				
Knorr 25	293	1456–1518	4	8°58.0′N	54°04.3′W	ES	27. 2.72

Dall (1886) records valves from Cape San Antonio (1833 m) and from the Yucatan Strait (1170 m), while James (1972) also records shells from the North East Gulf of Mexico in 1000 m and between 1097–1189 m. Shallow water records by Fischer-Piette (1973) from Calypso Stations 48 & 88 at depths of 40 m and 39 m respectively must be suspect.

DESCRIPTION (Figs. 51a, b & c). Shell ovate-triangular, moderately strong, moderately inflated, rostrum extended, regular, broad, concentric ridges, approximately equilateral; umbo, slightly raised, beaks medially directed, position changes with increasing size; dorsal margin convex, antero-

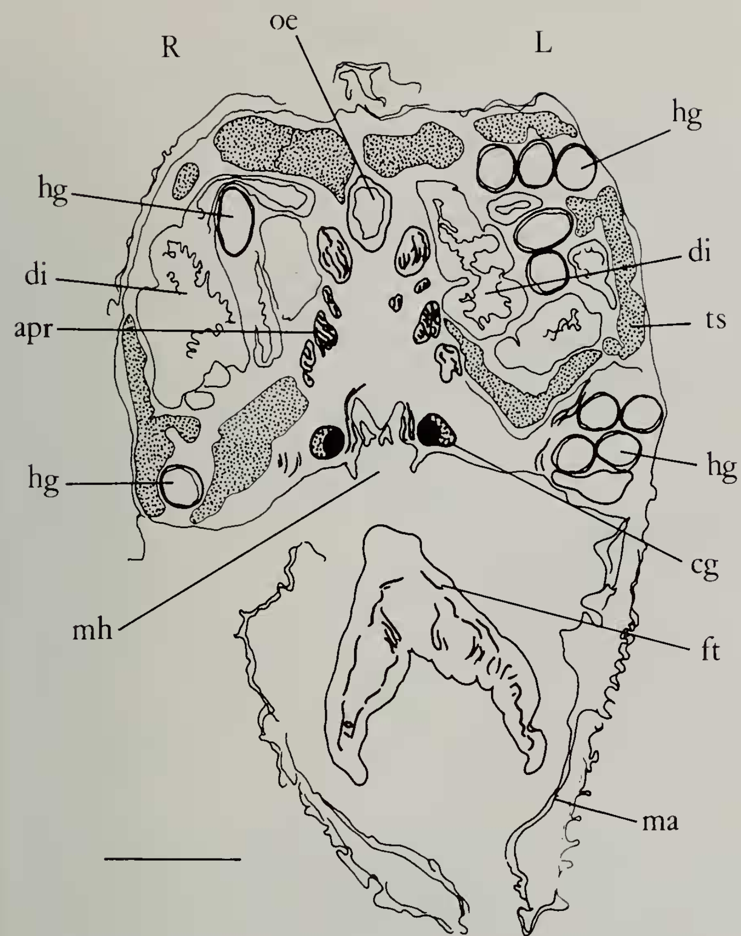

Fig. 53 *Ledella solidula*: Transverse ventral section of body immediately anterior to the stomach. (Scale = 0.1 mm).

dorsal margin slopes sharply to form curve with anterior edge, postero-dorsal margin slopes more gradually from umbo, margin almost straight in large specimens but usually slightly convex, angled slightly at distal end of hinge plate, keel extends from umbo to tip of sharp pointed rostrum with concentric ridges making a right angle at its crest, postero-ventral margin conspicuously sinuous, ventral margin long, moderately convex; hinge plate broad, strong, relatively long, anterior and posterior parts with approximately nine chevron-shaped teeth (number varies with length), six distal teeth are large and strong, proximal teeth progressively smaller; ligament amphidetic, internal, goblet-shaped; adductor muscle scars visible.

Larval shell length 245 μm, maximum recorded length 5.78 mm.

MORPHOLOGY. Although similar to *L. galathea*, the organization of the hind gut differs from the others previously described. In other details the morphology is similar to other species described above. (Fig. 52).

The anterior bean-shaped adductor muscle is approximately twice the size of the oval posterior muscle. The gills are moderately small, with up to 12 plates in each demibranch. The labial palps are relatively large with 14–24 ridges and, as in the case of the gill plates, the number being dependent on the size of the individual. The palp proboscides are long and moderately thin.

The foot is large with a small 'byssal' gland. The pedal ganglion is large while the cerebral and visceral ganglia are long and thin and moderate in size.

The stomach lies anterior in the body. The style sac penetrates the lower half of the foot posterior to the pedal ganglia. The hind gut extends further into the foot to a point immediately dorsal to the byssal gland. From there it curves back on itself posterior to the stomach to the dorsal body margin where it passes the right side. From there it takes an anterior course to the anterior adductor muscle where it crosses to the left side to form four coils (Fig. 53). These lie in the anterior half of the body between the anterior adductor muscle and a line vertical to the umbo. After forming the coils the hind gut returns to the right side again, immediately posterior to the anterior adductor, and from there dorsally to the anus.

One male specimen (4.8 mm total length) from Station 293 was found to be in the process of releasing sperm. These were present in the mantle cavity, on the gills and within the siphon. The volume of body occupied by the testis was estimated at 17.0%.

The change in shell shape with growth is particularly marked in this species (Figs. 54 & 55). In the largest specimens there is a slight change in the direction of growth at the ventral edge (Fig. 51) although this is to a much lesser extent than that described in the case of *L. ultima* (p. 161). With increasing length, the rostrum becomes more elongate and may be pointed and the dorsal margin becomes more convex.

A large number of dead shells were present in the sample from Station 118 and the length of these were compared with those of live specimens (Fig. 56). In the case of valves only one was recorded in the case of those joined by hinge and ligament and only half of the total for each size of the single valves (+ 1 in case of an odd number). From this it is clear that the vast majority of dead shells are at the maximum size of the species with few at lengths below 2 mm which would appear to support the contention that mortality patterns in deep sea bivalves differs markedly from those in shallow waters where the greatest mortality occurs in juveniles (see Oliver & Allen 1980).

DISTRIBUTION. Surinam Basin, Gulf of Mexico and Bermuda Slope from 1000–1830 m.

Ledella acuminata (Jeffreys 1870)

LECTOTYPE. USNM No. 199672.

TYPE LOCALITY. Mediterranean 550 metres.

SYNONYMY. *Leda acuminata* Jeffreys 1870 *Ann. Mag. nat. Hist.* Ser. 4, *6*, p. 69.
Leda messanesis Jeffreys 1879 *Proc. zool. Soc. Lond.* 1879, p. 576 (in part).
Yoldiella acuminata Warén 1978 *Sarsia, 63,* p. 215. Figs. 1, 2, 10 & 11.

MATERIAL. Collections from the Porcupine Expedition in the USNM & BMNH have been examined.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		BAY OF BISCAY					
Sarsia	56	641	1	43°43.0′N	3°47.8′W	ED	19. 7.67
	63	1336	1	46°17.5′N	4°45.2′W	ED	24. 7.67
	66	1427	1	46°16.3′N	4°44.0′W	ED	25. 7.67
Thalassa	Z397	511	2	47°33.8′N	7°12.6′W	GBO	22.10.73
	Z399	825	1	47°34.8′N	7°18.1′W	GBS	22.10.73
	Z400	1175	1	47°33.4′N	7°19.0′W	GBS	22.10.73
	Z413	805	3	48°03.1′N	8°29.4′W	PBS	24.10.73
	Z414	650	7	48°05.0′N	8°29.8′W	PBS	24.10.73

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	Z415	386	1	48°07.2′N	8°26.2′W	PBS	24.10.73
	Z424	475	2	48°27.9′N	9°44.3′W	PBS	25.10.73
	Z435	1050	1	48°39.7′N	9°53.2′W	PBS	26.10.73
		MEDITERRANEAN					
Atlantis II–59.	211	500–509	90	33°57.0′N	15°08.2′W	ES	2. 9.70

The shell morphology has been well described by Warén (1978) and requires little further addition.

DESCRIPTION (Figs. 57 & 58). Shell thin, elongate-oval with pointed rostrum, ornament of fine, concentric ridges becoming more conspicuous towards ventral margin; dorsal margin weakly convex, antero-dorsal margin, gradual curve, slopes to smooth curve with anterior margin, proximal postero-dorsal margin relatively straight at posterior limit of hinge plate, slope increases to form convex dorsal margin of elongate rostrum, postero-ventral margin sinuous, ventral margin long, moderately smooth curve; umbo usually anterior to mid line, moderately low in profile, medially directed; low rounded keel extends from umbo to top of rostrum, concentric ridges form an approximate right angle at keel; anterior and posterior hinge plates strong, broad, elongate, each with 7–11 chevron-shaped teeth; ligament amphidetic, largely internal, goblet-shaped with small external extensions on either side of umbo; adductor scars visible.

Larval shell length 200 µm, maximum recorded length 4.93 mm.

MORPHOLOGY. The basic form of the body is similar to that of other species of *Ledella* with a hind gut with a coiled configuration on the left side of the body (Fig. 59).

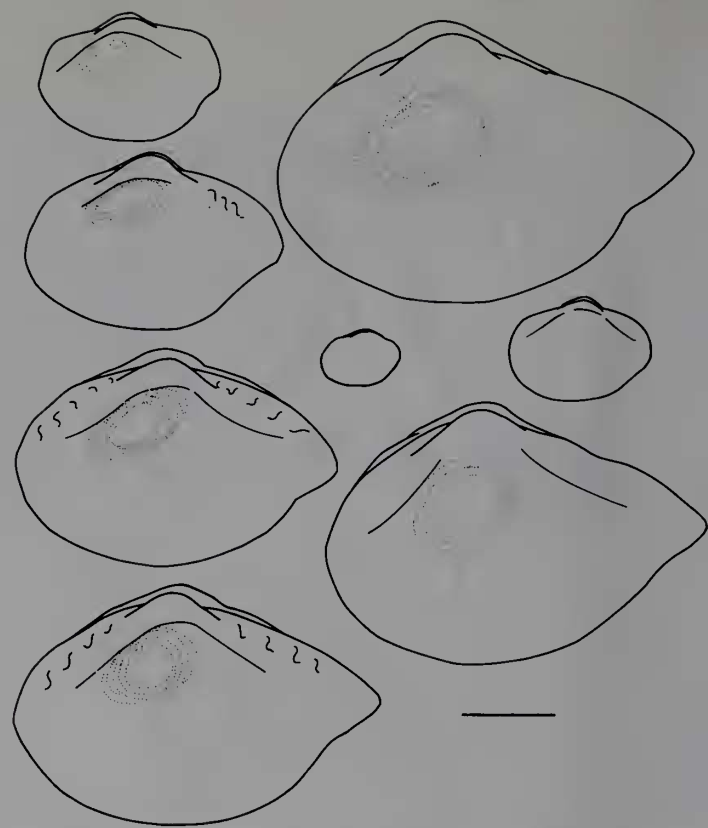

Fig. 55 *Ledella solidula*: Growth series of shells from Station 118 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

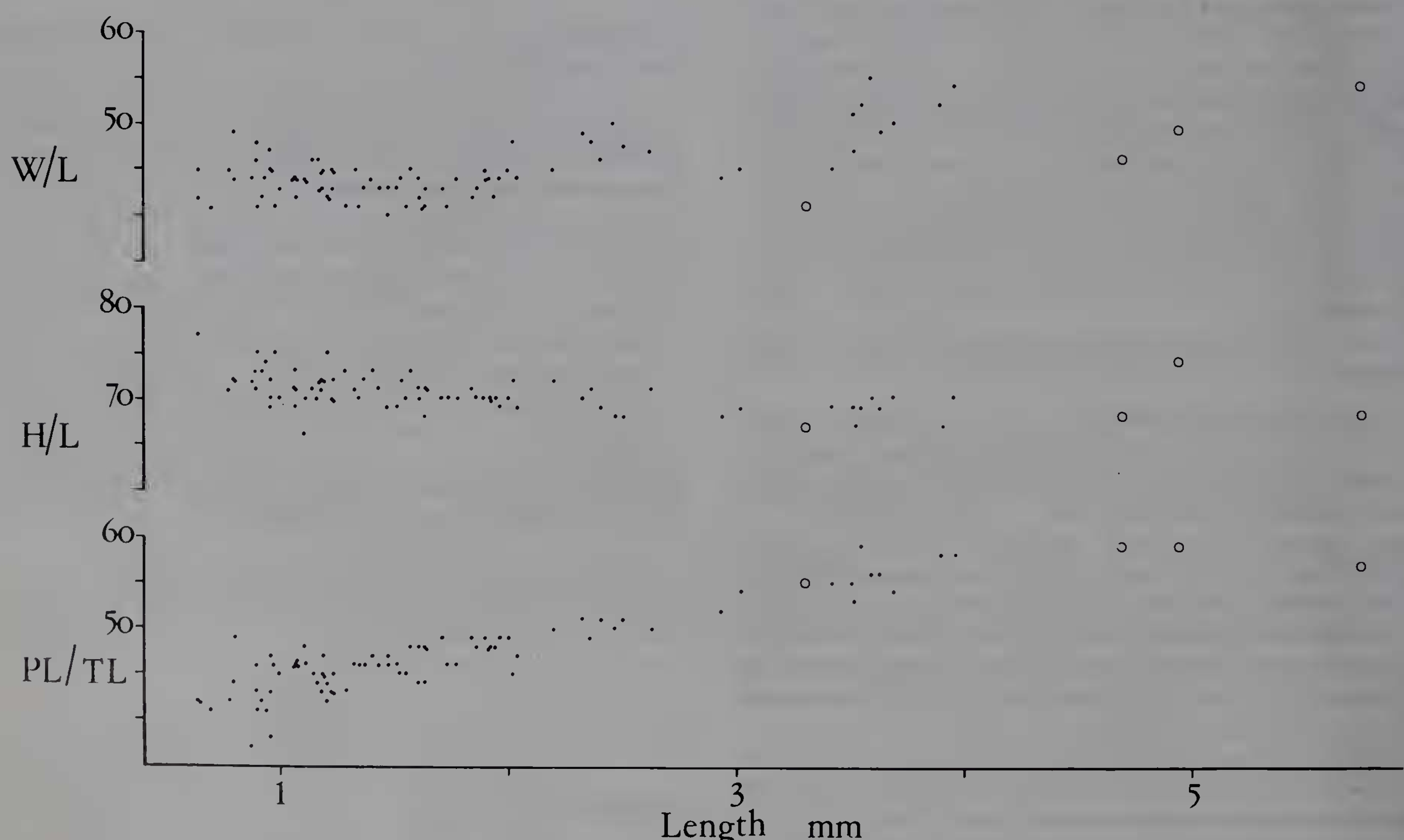

Fig. 54 *Ledella solidula*: An analysis of change in shape with growth as shown by the ratios posterior umbo length/length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 293 (open circles) and Station 118 (points).

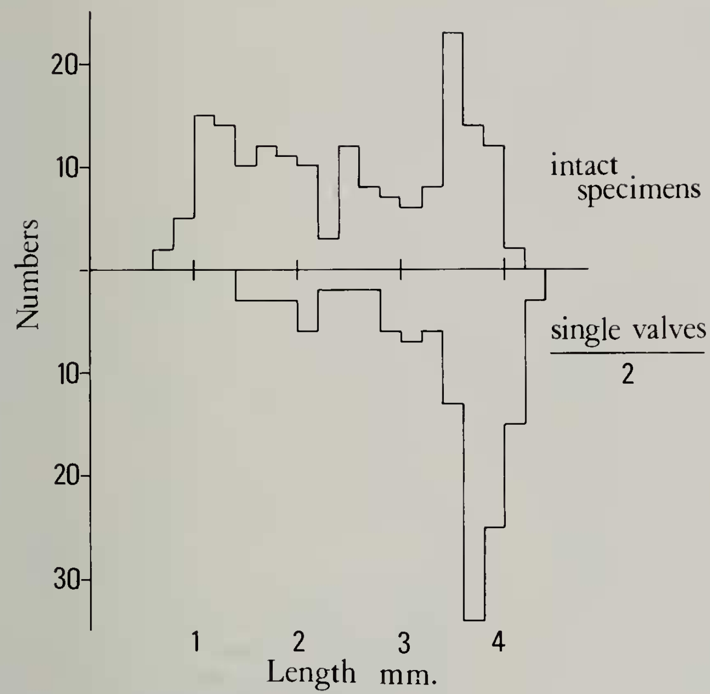

Fig. 56 *Ledella solidula*: Comparative histograms of size range of living and dead shells (see text for further explanation).

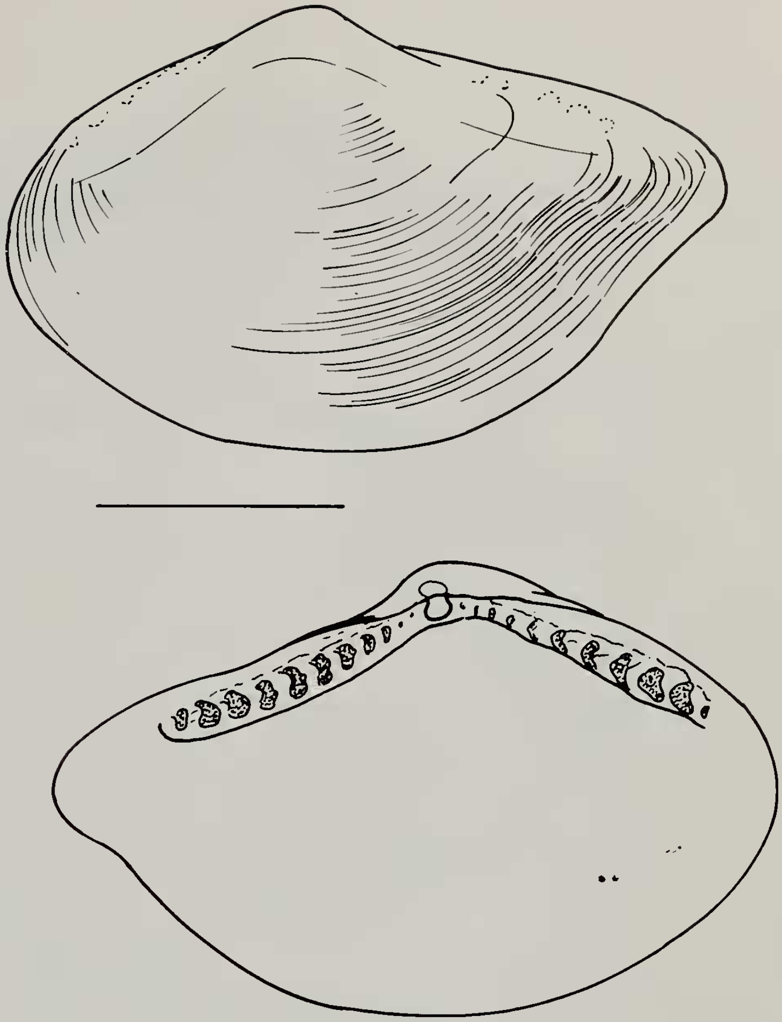

Fig. 57 *Ledella acuminata*: Left lateral external view of lectotype (USNM No. 199672) 310 fm. Mediterranean and lateral internal view of lectotype. (Scale = 1 mm).

The adductor muscles differ in size and shape. The anterior muscle is 2 or 3 times the size of the posterior, it is bean-shaped with the longitudinal axis parallel to the anterior margin. The posterior adductor is elongate-oval in shape with the longitudinal axis parallel to the dorsal margin. The siphon is moderately large and muscular with the siphonal tentacle usually inserted to the right at the base of the siphon. The feeding aperture is well developed.

The species has the greatest number of labial palp ridges of any species described here (22–28 depending on the size of the animal), however, the area of body covered by the palps is similar to that of most other species. The palp proboscides are large, long and in the contracted state, much folded. The gills are moderately well developed with 22–26 filaments. Posterior of the foot the inner demibranchs lie in close proximity to one another, those close to the base of the siphon appear to be interlocked.

The foot is large, peripherally deeply papillate and with an extended heel. The 'byssal' gland is large. The pedal retractor muscles are similar to those described for *L. pustulosa*. The cerebral and visceral ganglia are relatively small and cylindrical in shape while the pedal ganglia are large.

The stomach and style sac are large. The hind gut follows a course similar to that described for *L. solidula* with a single loop to the right and four or five coils to the left of the body. The number of coils immediately visible through the translucent shell varies from 2–5, coils overlain by others often being masked in lateral view (Fig. 60). In a subsample of nine sectioned individuals taken from Station 211 the number of coils varied, 5 specimens having 5 coils, the remaining 4 with 4 coils. The outline shape of the coils is variable. Hind gut morphology is very similar to that seen in *Tindariopsis acinula* (Dall): (Sanders & Allen, 1977).

Shell changes shape with increasing length (Fig. 60 & 61). The rostrum becomes increasingly prominent with a corresponding change in the relative position of the umbo, i.e. becoming more anterior with increasing length. The width of the animal relative to total length changes little during growth, but there is a slight but gradual decrease in relative height. (Fig. 61). *L. acuminata* is one of the least inflated species of the genus (Fig. 3f) with an average ratio of width to length of 0.37 (Sta. 211).

In section the smallest specimen with recognizable gonad tissue was 2.3 mm length. The number of eggs varies from 159 in an individual 3.00 mm in length to 587 in an individual 4.6 mm. The maximum length of the eggs was relatively constant in specimens from Station 211 (140–148 µm) although in general the larger the individual the greater the area of body covered by gonad. There is an approximately equal number of males and females (Fig. 62).

Distribution. Bay of Biscay and Mediterranean.

Depth range. 475–1427 m.

Ledella ultima (Smith 1885)

Lectotype. BM(NH) 1887.2.9.3354; 1 left valve, designated herein, Paralectotypes: 2 right valves. (Holotype *L. bushae* USNM No. 52 156, type locality off Martha's Vineyard about 4700 m. Holotype *L. crassa* Zoological Museum University of Copenhagen (ZMUC), type locality 'Galathea' Sta. 24, off W. Africa, 3°54.0'N, 8°22.0'W, 3196 m.

Fig 58 *Ledella acuminata*: Left lateral external view of specimen from Station 211 and lateral internal view of specimen from Station 211 to show detail of hinge plate. (Scale = 1 mm).

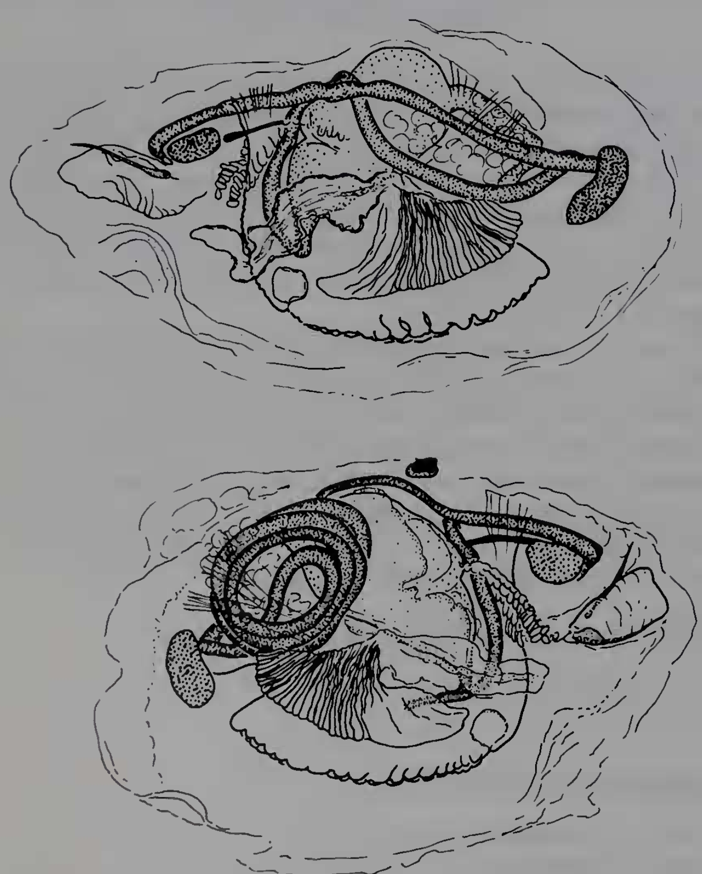

Fig. 59 *Ledella acuminata*: Lateral views of specimen from the left and right sides with the shell removed to show the arrangement of the body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

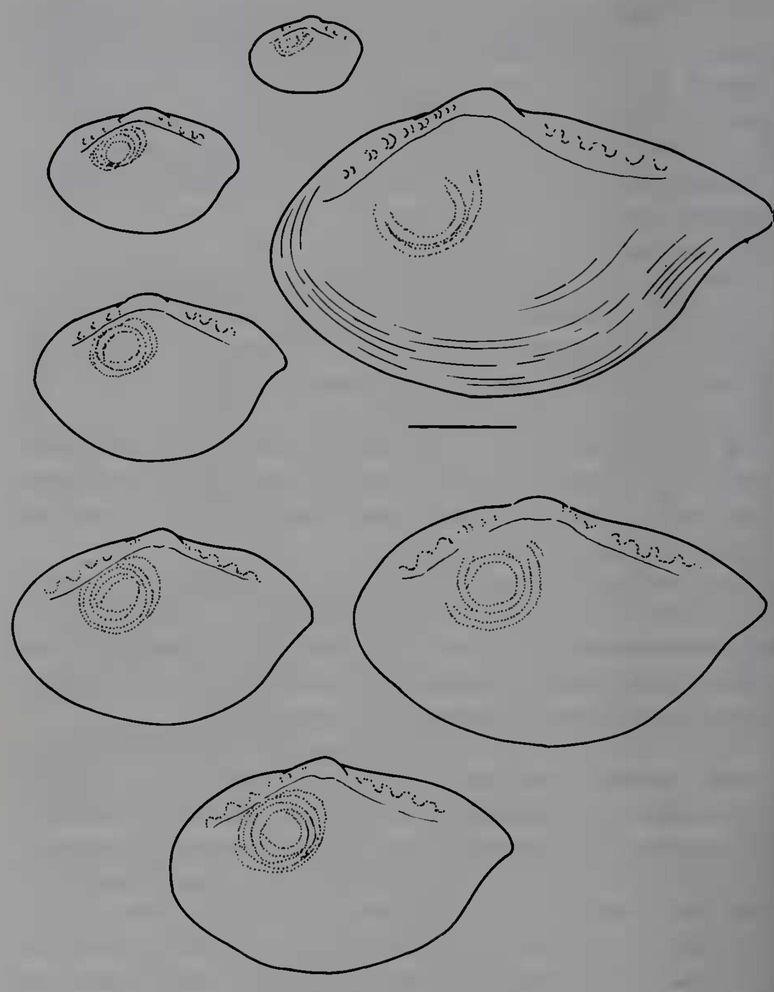

Fig. 60 *Ledella acuminata*: Growth series of shells from Station 211 in lateral outline to show change in shape with increasing age and with details showing hind gut and hinge as seen through the transluscent shell. (Scale = 1 mm).

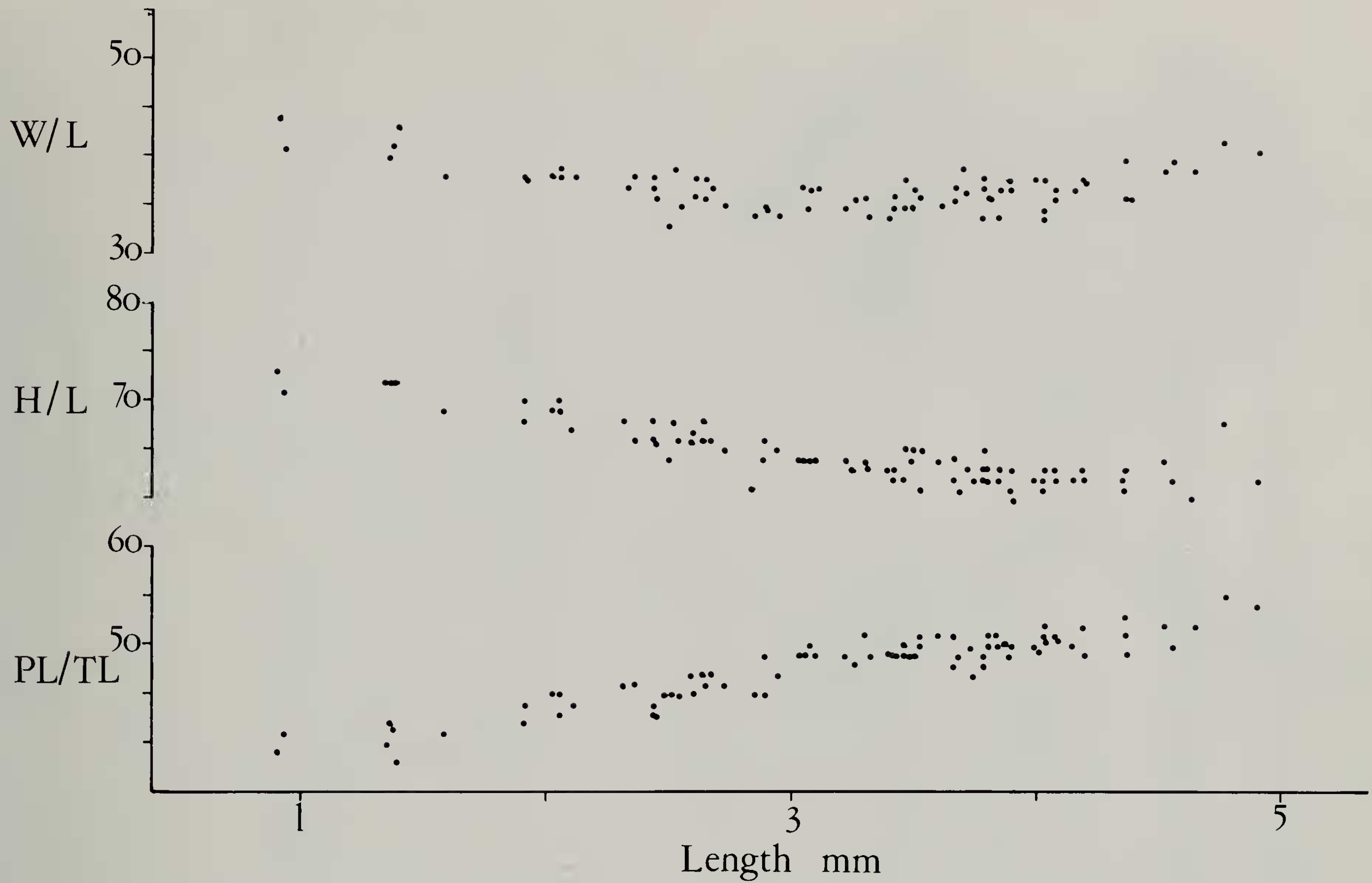

Fig. 61 *Ledella acuminata*: Analysis of change in shape with growth as shown by the ratios posterior umbo length/total length (PL/TL), height/length (H/L), width/length (W/L) plotted against length for specimens from Station 211.

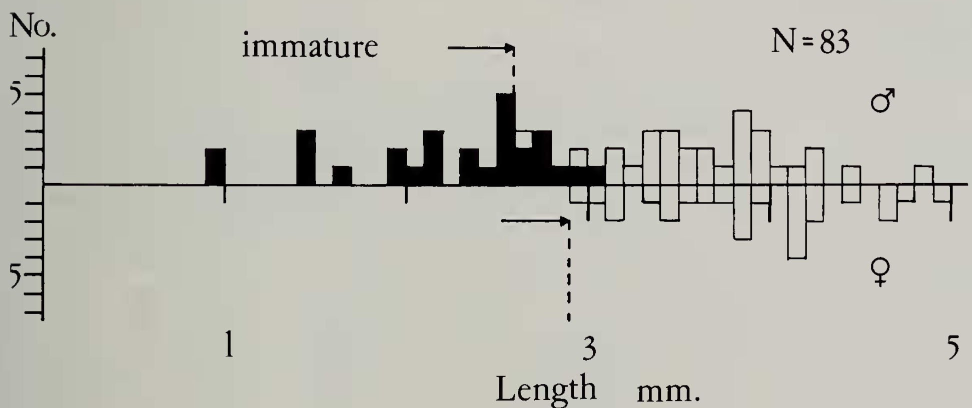

Fig. 62 *Ledella acuminata*: Histogram of specimens from Station 211, identified as immature (solid record) and maturing (open record) males and females as recorded through the transluscent shell.

TYPE LOCALITY. Challenger Sta. 5, 24°20.0′N., 24°28.0′W, 5011 m, Southwest of the Canary Islands.

SYNONYMY. *Leda ultima* Smith, 1885. *Exp. Chall. 13*, p. 324. Figured (no number) on p. 324.
Ledella messanensis Verrill & Bush, 1897. *Am. J. Sci. 54*, Fig. 13, 18 (*non Leda messanensis* Seguenza MS, *in* Jeffreys, 1870).
Nuculana ultima (Smith): Clarke, 1961 *Bull. Mus. Zool. Harv. 125*, p. 375.
Ledella crassa Knudsen, 1970. *Galathea Rep. 11*: pp. 30–32, Fig. 12, 13, pl. 3. Fig. 1.
Ledella bushae Warén, 1978. *Sarsia 63*, p. 213, Figs. 8 & 9.
Ledella bushae Warén: Warén, 1981. *Bull. Zool. Nom. 38*, p. 134–37.

This is the most common species of *Ledella* present in the Atlantic and it has a widespread distribution. There are multiple descriptions of the species under different names.

Our extremely large collections show that *L. ultima* (Smith) from the Canaries (named *L. crassa* by Knudsen (1970)), from the north west Atlantic (named *L. messanensis* by Verrill & Bush (1897, 1898)), and *L. bushae* (named by Warén (1978) and later confirmed as type species following Warén 1981) are one and the same species. Detailed observations from our own material from these and other localities show two points of difference from the earlier descriptions:– (a) the maximum number of teeth is greater than previously recorded (see below) and (b) a thickened ventral edge is present in older specimens particularly, but not exclusively, those collected off West Africa. Both of these differences simply relate to the large numbers in the present collections which extend the size range of the species.

MATERIAL.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		NORTH AMERICAN BASIN					
Atlantis	111	3742	17	37°59.0′N	69°32.0′W	AD	22. 5.61
264	112	3752	1	38°05.0′N	69°36.0′W	AD	24. 5.61
273	JJ1	4436	14	37°27.0′N	68°41.0′W	AD	2.10.61
	HH2	2488	2	39°26.0′N	70°34.0′W	AD	3.10.61
277	JJ3	4540	19	37°13.1′N	68°39.6′W	AD	25. 6.62
Atlantis II	69	4663	5	36°15.0′N	67°51.0′W	AD	23. 8.64
12	70	4680	1086	36°23.0′N	67°58.0′W	ET	23. 8.64
	73	1330–1470	1	39°46.5′N	70°43.3′W	ET	25. 8.64
Chain	77	3806	1423	38°00.7′N	69°16.0′W	ET	30. 6.65
50	78	3833	250	38°00.8′N	69°18.7′W	ET	30. 6.65
	80	4970	5	34°49.8′N	60°34.0′W	ET	2. 7.65
	81	5042	3	34°41.0′N	66°28.0′W	ET	2. 7.65
	84	4749	702	36°24.4′N	67°56.0′W	ET	4. 7.65
	85	3834	1045	37°59.2′N	69°26.2′W	ET	5. 7.65
Atlantis II	92	4694	209	36°20.0′N	67°56.0′W	ET	13.12.65
17	93	5007	1	34°39.0′N	66°26.0′W	ET	14.12.65
	95	3753	134	38°33.0′N	68°32.0′W	ET	17.12.65
Chain 58	101	4700	321	36°24.2′N	68°01.3′W	ET	3. 5.66
Atlantis II	108	4739	8	00°00.0′N	00°00.0′W	ET	7. 8.66
23	109	4750	554	00°00.0′N	00°00.0′W	ET	8. 8.66
	110	4750	13	00°00.0′N	00°00.0′W	ET	8. 8.66
	112	2900	1	00°00.0′N	00°00.0′W	ET	9. 8.66
Atlantis II	121	4800	327	35°50.0′N	65°11.0′W	ET	21. 8.66
24	122	4833	108	35°50.0′N	64°57.5′W	ET	21. 8.66
				−35°53.0′N	−64°58.0′W		
	123	4853	377	37°29.0′N	64°14.0′W	ET	22. 8.66
	124	4862	179	37°26.0′N	63°59.5′W	ET	22. 8.66
				−37°25.0′N	−63°58.0′W		
	125	4825	498	37°24.0′N	65°54.0′W	ET	23. 8.66
				−37°26.0′N	−65°50.0′W		
	126	3806	56	39°37.0′N	66°47.0′W	ET	24. 8.66
				−39°37.5′N	−66°44.0′W		
Atlantis II	175	4667–4690	387	36°36.0′N	68°29.0′W	ES	29.11.67
40				−36°36.0′N	−68°31.0′W		
		GUINEA BASIN					
Walda	DS20	2514	1	02°32.0′S	08°18.1′E	DS	
	DS31	4279	43	03°17.5′N	02°01.7′E	DS	
		CAPE VERDE BASIN					
Atlantis II	147	2934	29	10°38.0′N	17°52.0′W	ES	6. 2.67
31	148	3814–3828	197	10°37.0′N	18°37.0′W	ES	7. 2.67
	149	3861	579	10°30.0′N	18°18.0′W	ES	7. 2.67
		BRAZIL BASIN					
Atlantis II	156	3459	1	00°46.0′S	29°28.0′W	ES	14. 2.67
31				−00°46.5′S	−29°24.0′W		
		ARGENTINE BASIN					
Atlantis II	242	4382–4402	3	38°16.9′S	51°56.1′W	ES	13. 3.71
60	256	3906–3917	75	37°40.9′S	52°19.3′W	ES	24. 3.71
	259	3305–3317	4	37°13.3′S	52°45.0′W	ES	26. 3.71
		WEST EUROPE BASIN					
Chain 106	326	3859	7	50°04.9′S	14°23.9′W	ES	22. 8.72
				−50°05.3′S	−24°24.8′W		
	328	4400	45	50°04.7′S	15°44.8′W	ES	23. 8.72
	330	4632	12	50°43.5′S	17°51.7′W	ES	24. 8.72
				−50°43.4′S	−17°52.9′W		
	335	3882–3919	22	40°25.3′S	46°30.0′W	ES	31. 8.72
Jean Charcot	DS23	4734	5	46°32.8′N	10°21.0′W	ES	26.10.72
(Polygas)	DS20	4226	1	47°33.0′N	09°36.7′W	ES	24.10.72
(Biogas II)	DS30	4106	1	47°38.3′N	09°33.9′W	DS	18. 4.73
(Biogas III)	DS45	4260	1	47°33.9′N	09°38.4′W	DS	27. 8.73
	DS46	4521	6	46°28.6′N	10°23.0′W	DS	29. 8.73
(Biogas IV)	DS53	4425	35	44°30.4′N	04°56.3′W	DS	19. 2.74
	DS54	4659	19	46°31.1′N	10°29.1′W	DS	21. 2.74
	DS55	4125	16	47°34.9′N	09°40.9′W	DS	22. 2.74
	DS56	4050	3	47°32.7′N	09°28.2′W	DS	23. 2.74
(Biogas V)	DS66	3480	1	47°28.2′N	09°00.0′W	DS	16. 6.74
	DS68	4550	2	46°26.7′N	10°23.9′W	DS	19. 6.74
	DS69	4510	6	44°21.9′N	04°52.4′W	DS	20. 6.74
(Biogas VI)	DS75	3250	4	47°28.1′N	09°07.8′W	DS	22.10.74
	DS76	4228	30	47°34.8′N	09°33.3′W	DS	23.10.74
	DS77	4240	6	47°31.8′N	09°34.6′W	DS	24.10.74
	DS78	4706	29	46°31.2′N	10°23.8′W	DS	25.10.74
	DS79	4715	21	46°30.4′N	10°27.1′W	DS	26.10.74
	DS80	4720	6	46°29.5′N	10°29.5′W	DS	27.10.74
	DS81	4715	4	46°28.3′N	10°24.6′W	DS	27.10.74
	DS84	4466	82	44°30.0′N	04°53.9′W	DS	29.10.74
	DS85	4462	16	44°23.2′N	04°50.8′W	DS	30.10.74
	CP13	4134	1	47°34.4′N	09°38.0′W	CP	23.10.74
	CP14	4237	4	47°32.0′N	09°35.9′W	CP	23.10.74
	CP16	4825	3	46°27.3′N	10°25.8′W	CP	25.10.74
	CP17	4706	2	46°30.8′N	10°19.5′W	CP	26.10.74
	CP20	4459	1	44°23.2′N	04°51.4′W	CP	29.10.74
	CP21	4453	1	44°21.2′N	04°49.3′W	CP	30.10.74
	CP22	4475	6	44°22.9′N	04°54.8′W	CP	30.10.74
Jean Charcot	CP10	4823	11	48°25.5′N	15°10.7′W	DS	31. 7.76
(Incal)				−48°26.3′N	−15°09.8′W		
	DS11	4823	5	48°18.8′N	15°11.5′W	DS	1. 8.76
				−48°13.6′N	−15°12.0′W		
	WS03	4829	41	48°19.2′N	15°23.3′W	WS	1. 8.76
				−48°19.1′N	15°22.5′W		
	CP11	4823	5	48°20.4′N	15°14.6′W	CP	1. 8.76
				−48°21.2′N	−15°13.7′W		
	0S02	4829	14	48°19.2′N	15°15.9′W	OS	2. 8.76
				−48°19.1′N	−15°15.5′W		
	WS04	4829	1	48°18.9′N	15°15.9′W	WS	2. 8.76
				−48°19.1′N	−15°15.5′W		
	WS07	4281	21	47°30.6′N	09°37.1′W	WS	7. 8.76
				−47°31.2′N	−09°35.7′W		
	0S05	4296	5	47°31.3′N	09°34.6′W	OS	
				−47°32.2′N	−09°34.7′W		
	DS14	4254	8	47°32.6′N	09°35.7′W	DS	7. 8.76
				−47°32.9′N	−09°35.1′W		
	DS15	4211	3	47°33.4′N	09°39.1′W	DS	8. 8.76
				−47°33.8′N	−09°38.5′W		
	WS0S	4287	61	47°30.5′N	09°33.7′W	WS	9. 8.76
				−47°29.3′N	−09°34.1′W		
	0S06	4316	27	46°27.3′N	09°36.2′W	OS	9. 8.76
				−47°27.9′N	−09°36.0′W		
	DS16	4268	14	47°29.8′N	09°33.4′W	DS	9. 8.76
				−47°30.3′N	−09°33.4′W		
	0S07	4249	22	47°31.8′N	09°34.3′W	OS	10. 8.76
				−47°31.3′N	−09°34.3′W		
	KR17	4268	1	47°31.2′N	09°32.0′W	KR	10. 8.76
				−47°31.3′N	−09°34.3′W		
	WS09	4277	61	47°28.8′N	09°34.0′W	WS	10. 8.76
				−47°27.9′N	−09°34.0′W		
	WS10	4354	149	47°27.3′N	09°39.9′W	WS	11. 8.76
				−47°28.2′N	−09°39.9′W		
	0S08	4327	12	47°29.8′N	09°39.2′W	OS	11. 8.76
				−47°29.5′N	−09°38.8′W		
		VEMA FRACTURE					
Jean Charcot	DS01	5097	1	10°57.2′N	45°07.6′W	DS	14.11.77
(Biovema)				−10°57.2′N	−45°07.1′W		
	DS03	5150	21	10°47.1′N	42°40.74′W	DS	16.11.77
				−10°47.19′N	−42°40.35′W		
	DS04	5100	18	10°46.38′N	42°41.38′W	DS	17.11.77
				−10°46.76′N	−42°41.11′W		
	KR05	5100	2	10°47.45′N	42°40.34′W	KR	17.11.77
	DS05	5100	32	10°45.97′N	42°40.29′W	DS	18.11.77
				−10°46.08′N	−42°39.85′W		
	CP05	5100	2	10°46.23′N	42°40.41′W	CP	19.11.77
				−10°46.36′N	−42°39.75′W		
	KG12	5100	1	10°47.5′N	42°40.41′W	KG	20.11.77
	DS09	5875	57+ 1V	11°36.4′N	32°51.8′W	DS	25.11.77
				−11°37.1′N	−32°51.3′W		

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
	DS10	5875	1	11°36.8′N −11°36.9′N	32°52.5′W −32°52.8′W	DS	25.11.77
	DS11	5867	89	11°37.5′N −11°37.6′N	32°53.8′W −32°52.8′W	DS	26.11.77
				CAPE BASIN			
Jean Charcot (Walvis)	DS01	5205–5240	2	33°53.9′N −33°53.9′S	05°05.9′W −05°06.4′W	DS	24.12.78
	DS02	5280	23	33°54.7′S	05°07.3′E −05°07.7′E	DS	25.12.78
	DS03	4657	1	33°21.8′S	02°40.4′E	DS	28.12.78
	KG05	5235	1	33°54.5′S	05°08.5′E	KG	25.12.78
	KG06	5210	1	33°54.2′S	05°09.2′E	KG	26.12.78
	KG08	5211	1	33°54.7′S	05°09.0′E	KG	26.12.78
	KG13	4560	1	33°22.7′S	02°36.8′E	KG	29.12.78
	DS05	4560	34	33°20.5′S	02°34.9′E	DS	30.12.78
	CP01	5040	3	33°53.6′S	05°06.7′E	CP	24.12.78
	CP05	4500	1	33°22.9′S −33°26.2′S	02°36.0′E −02°34.6′E	CP	30.12.78
	DS06	4585	22	33°24.5′S	02°32.9′E	DS	31.12.78
				ANGOLA BASIN			
(Walvis)	DS07	5100–5214	18	26°59.7′S −27°00.2′S	01°07.1′E −01°05.8′E	DS	3. 1.79
	DS08	5225	1	29°59.6′S	01°07.3′E	DS	5. 1.79
	DS09	5220	4	26°59.9′S −27°00.0′S	01°06.7′E −01°06.2′E	DS	6. 1.79

Although there are recent descriptions of the shell of *L. ultima* (Knudsen, 1970; Warén 1978) with the advantage of large numbers of samples and many thousands of specimens we have been able to assemble much more information on population variations.

DEPTH RANGE. 1330–5875 m

DESCRIPTION (Figs. 63–65). Shell solid, inflated, equilateral or almost so (postumbonal length 40–56% of total length depending on size), ornamented with sharp concentric ridges, slightly broader ventrally becoming narrow and fainter towards umbo with smooth area around umbo of varying width; umbos prominent, medially directed; dorsal margin convex, antero-dorsal margin forms smooth broad sloping curve with anterior margin, proximal postero-dorsal margin almost straight between umbo and distal end of hinge plate, distal margin short, deeply convex, forming relatively blunt rostrum which with posterior ventral sinuous margin gives 'hooked' appearance, ventral margin smooth curve, ill-defined rounded ridge from umbo to rostrum, in large specimens ventral margin may be thickened to form a flattened edge; hinge plate broad, solid, anterior and posterior plates each with up to 6–10 chevron teeth (number varying with size); internal ligament amphidetic rectangular in outline; adductor and pallial scars usually visible.

Larval shell length: 310 μm, maximum recorded shell length: 3.40 mm.

MORPHOLOGY. *Ledella ultima* differs from all other *Ledella* species described here in having the hind gut spirally coiled on the right side of the body (Figs. 66 & 67). The only other described *Ledella* species with this type of gut configuration is *L. kermadecensis* (Knudsen, 1970).

Other morphological features are similar to those described for the other species (Fig. 66). The mantle edge is relatively well developed, the inner fold being moderately broad. The combined siphon is not fused ventrally and is fairly small. A very fine siphonal tentacle, often difficult to observe, is attached close to the base of the siphonal embayment on the right or the left side. The anterior sense organ is more ventrally situated than in other species. The adductor muscles are large, approximately equal in size and round in shape. The gills lie parallel to the posterior dorsal margin with 8–11 gill plates. The labial palps are large with 14–20 ridges and with long, thin palp proboscides. The foot is large, deeply cleft with a very large 'byssal' gland (Fig. 68).

The stomach and style sac lie ventral to the umbos, they are relatively small, extending only into the upper third of the foot, posterior to the pedal ganglion. From the style sac the hind gut passes posterior and ventral to the pedal ganglion before retracing its path to the dorsal margin and then to the right side of the body where it forms a series of coils. These usually number 12 although exceptionally 13 have been observed. One individual was also observed with an additional loop to the left side of the body. The coils are stacked in an overlapping sequence dorsally and antero-laterally to the viscera. Some coils lie internal to the others, thus, a variable number of coils is immediately visible in lateral view, the most common number being eight. The extent of the area covered by the coils also varies, depending on the compactness and shape of the coils, which may be circular or oval in outline.

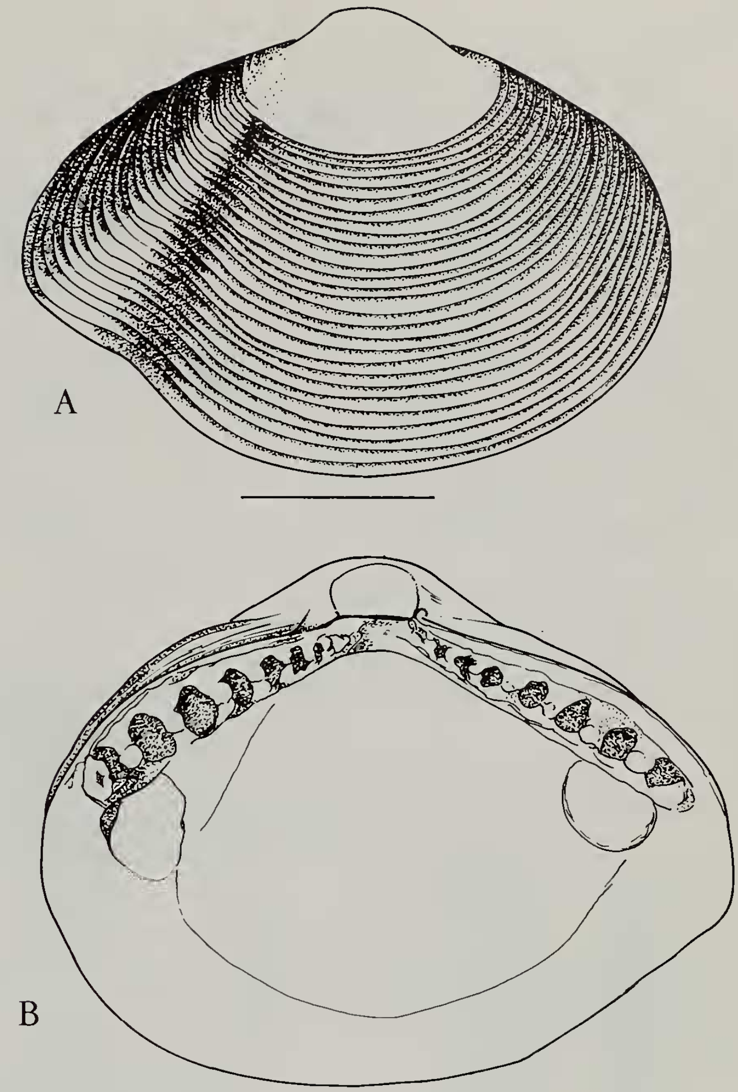

Fig. 63 *Ledella ultima*: (a) Right lateral external view of the Holotype specimen (BMNH No. 1887.2.9.3354) (note margin not thickened); (b) internal view of right valve of specimen with thickened margin from Station 175. (Scale = 1 mm).

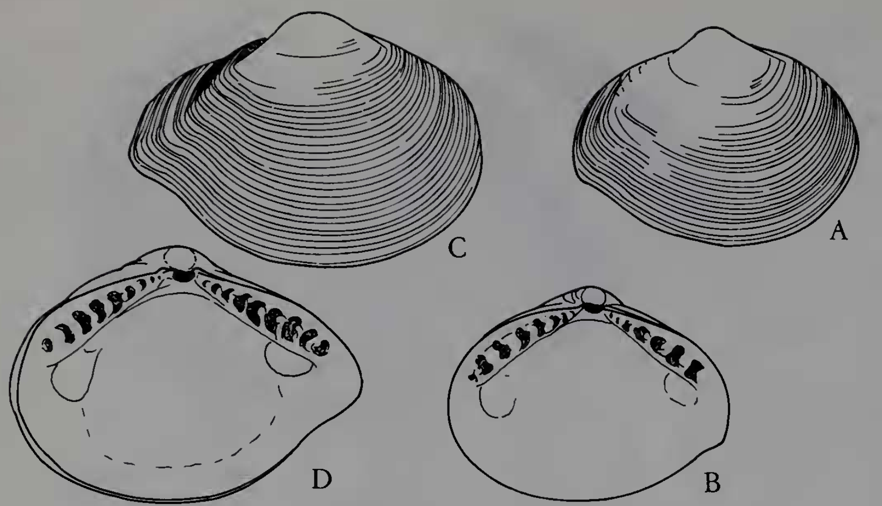

Fig. 64 *Ledella ultima*: (a) & (b) Right lateral external view and internal view of right valve of the type specimen of *L. bushae* (note margin not thickened), (c) & (d) Right lateral external view and internal view of right valve of type of *L. crassa* (note margin thickened). See p. 161 & Fig. 73 for details of variation in shape. (Scale = 1 mm).

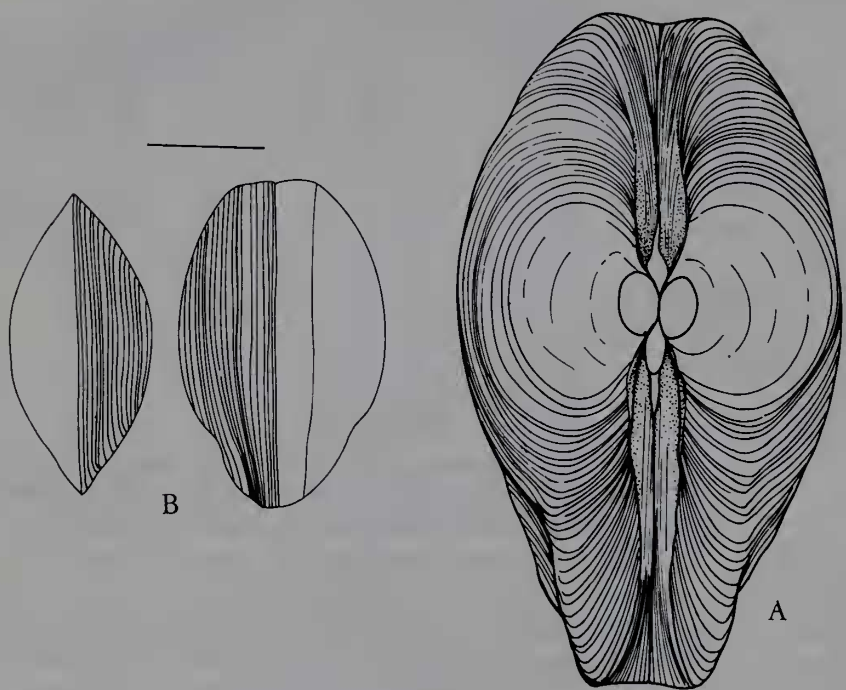

Fig. 65 *Ledella ultima*: (a) Dorsal view of shell with thickened margin from Station Biogas V DS69; (b) Ventral view of specimens of similar size, one with and the other without a thickened margin, from the North America Basin.

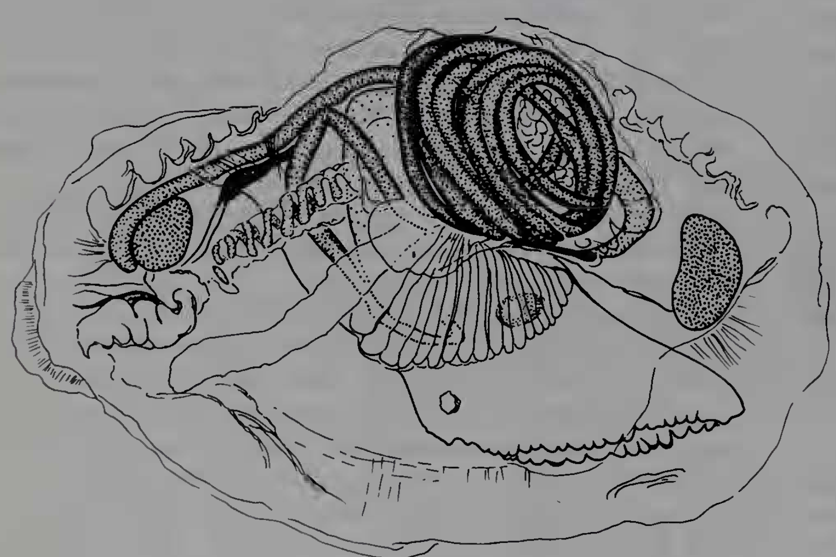

Fig. 66 *Ledella ultima*: Lateral view of specimen from the right side with shell removed to show the arrangement of body organs. For identification of parts see Fig. 42. (Scale = 1 mm).

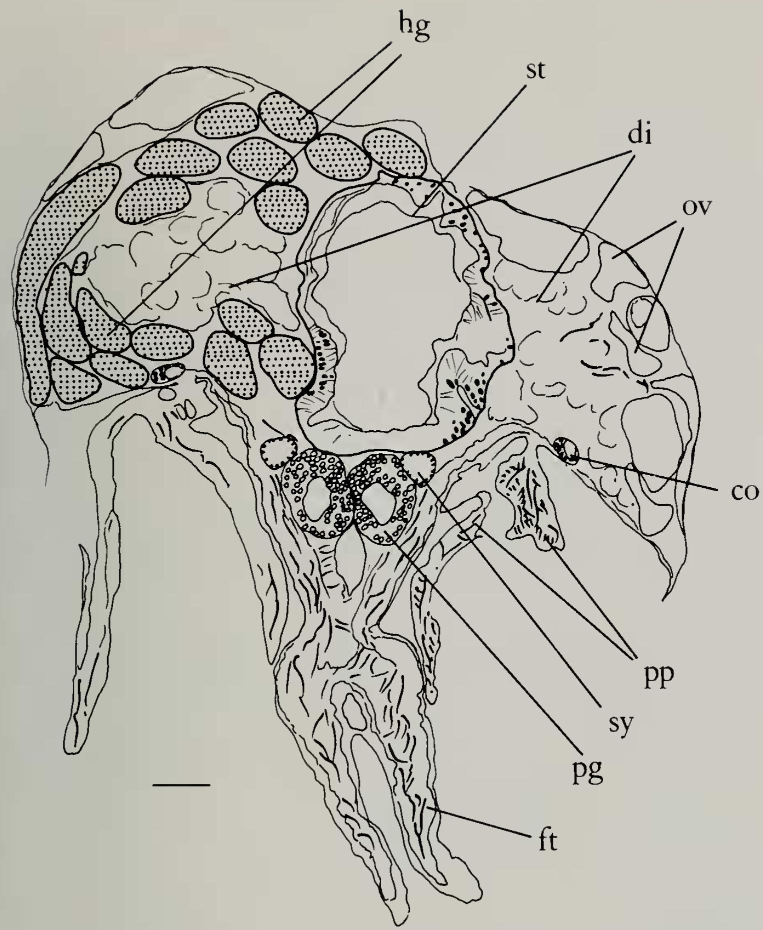

Fig. 67 *Ledella ultima*: Vertical transverse section through stomach and hind gut coil as viewed from anterior side (i.e. morphological right is topographically left). (Scale = 0.1 mm).

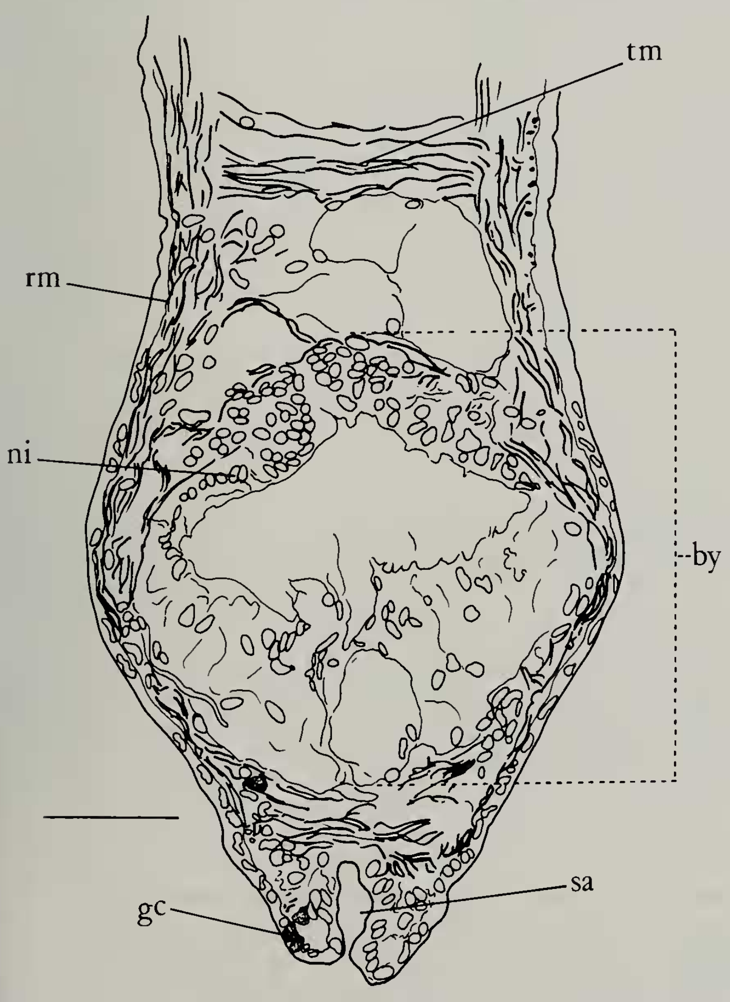

Fig. 68 *Ledella ultima*: Vertical transverse section through heel of the foot and the 'byssal' gland. (Scale = 0.1 mm).

The pedal ganglia are large (Fig. 67). The cerebral and visceral ganglia are smaller and club-shaped, the visceral ganglia lying anterior to the posterior adductor muscle.

The smallest individual recorded with discernible gonads was 2.4 mm in length. Development was assessed in two samples, one from the western Atlantic (Sta. 101) and the other from the eastern Atlantic (BGIV DS53). The maximum diameter of the ova in different mature individuals varied from 160–280 μm (Sta. 101) and from 220–255 μm (BGIV DS53). Ova were few in number, 6–29 per individual at both Stations most being in the left side of the body, diametrically opposite to the coils of the hind gut. Individuals from Station 101 with thickened shell margins (› 0.6 mm) were compared with ones without a thickened margin (‹ 0.1 mm) but of comparable total shell length. Overall fewer ova which tended to be smaller were present in those with no thickening of the margin (Table 1).

The percentage of the lateral body covered by testis ranged from 0.5% (2.5 mm total length) to 19% (2.9 mm total length) in individual specimens examined from Station BGIV DS53 and 4.5% (2.87 mm total length) to 16.5% (2.5 mm total length) at Station 101.

Table 1. Comparison of numbers of ova in specimens with and without thickened shell margins

Not Thickened			Thickened			
Shell length	Max Diam. of ova	Number of ova	Shell length	Max Diam. of ova	Number of ova	Thickness of ventral margin (mm)
2.79	160μm	6	2.79	210μm	20	0.82
2.81	220μm	9	2.81	210μm	29	0.90
2.83	160μm	8	2.81	240μm	14	1.64
2.89	240μm	10	2.83	260μm	11	0.90
			2.97	280μm	25	0.66*

* partially spent.

During the course of growth, there is little change in the relative position of the umbo. In very small individuals it is usually posterior to the midline but with increasing length, it becomes more central in position. Although there is a slight increase in height/length ratio with increasing length, considerable variation was observed. It should be noted that analysis of the width/length ratio is complicated by the thickening of the shell margin (Fig. 69).

Thickening of the shell margin to form a flattened edge may be present in individuals › 2.4 mm in length, however, not all individuals above this length exhibit thickening (Fig. 70). The maximum recorded thickening was 1.3 mm in an individual shell 2.5 mm in length. The feature is formed following a sharp change in the spiral angle of growth of the shell to produce a flattened edge. While not a unique occurrence among deep sea protobranchs it is by far seen at its most extreme in *Ledella ultima*. It is possible that it may be a feature of those specimens that are maturing for a second or more time.

Because of the multiplicity of names given to this species, various shell parameters from samples from different basins of the Atlantic were measured and compared (Figs. 69, 71, 72 & 73). The Stations selected were:- Walda DS31 (Guinea

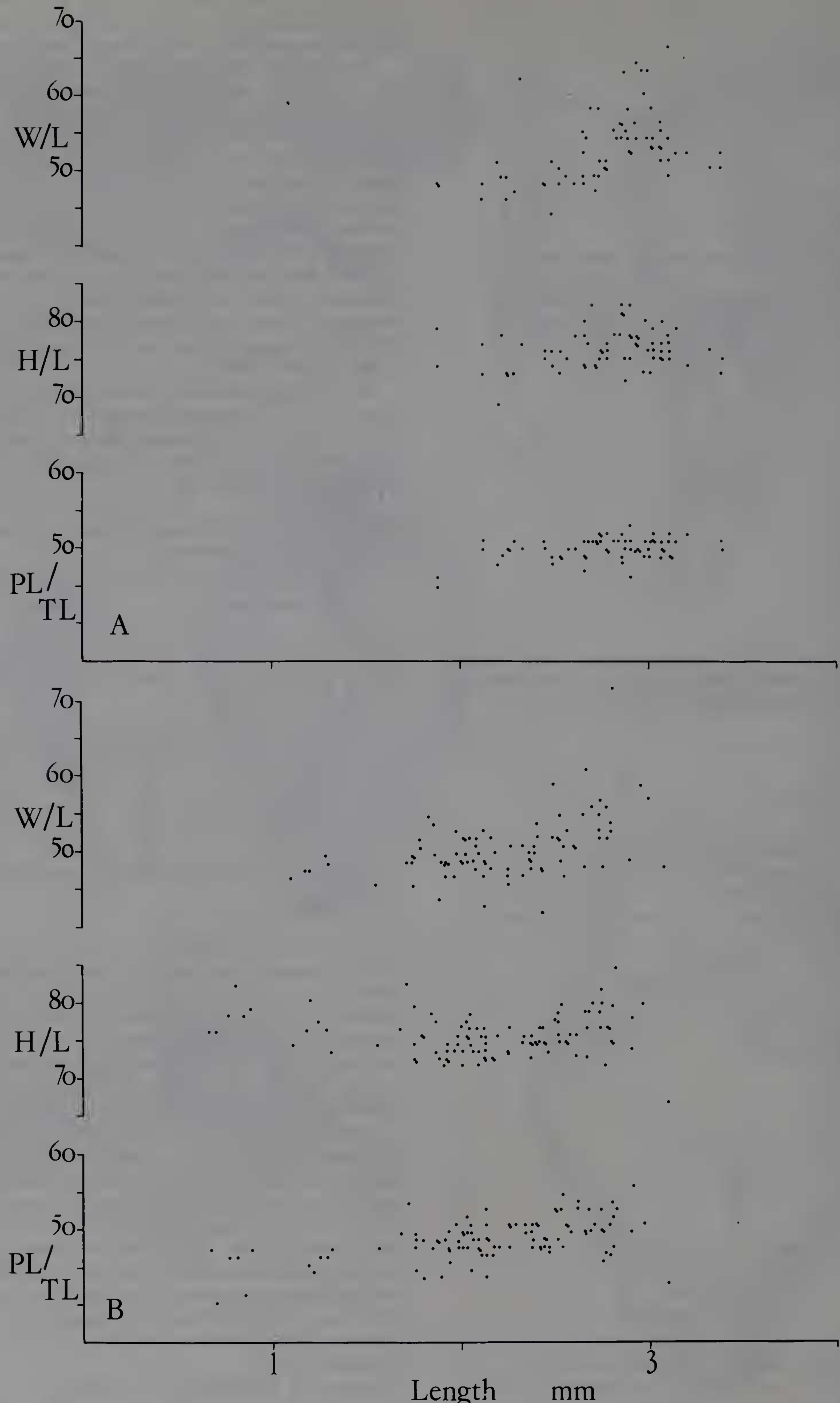

Fig. 69 *Ledella ultima*: (a) & (b) Analysis of change in shape with growth as shown by the ratios posterior umbo length/total length (PL/TL), height/length (H/L) and width/length (W/L) plotted against length for specimens from Station 122 and Station Biogas VI DS84. Fig. 70.

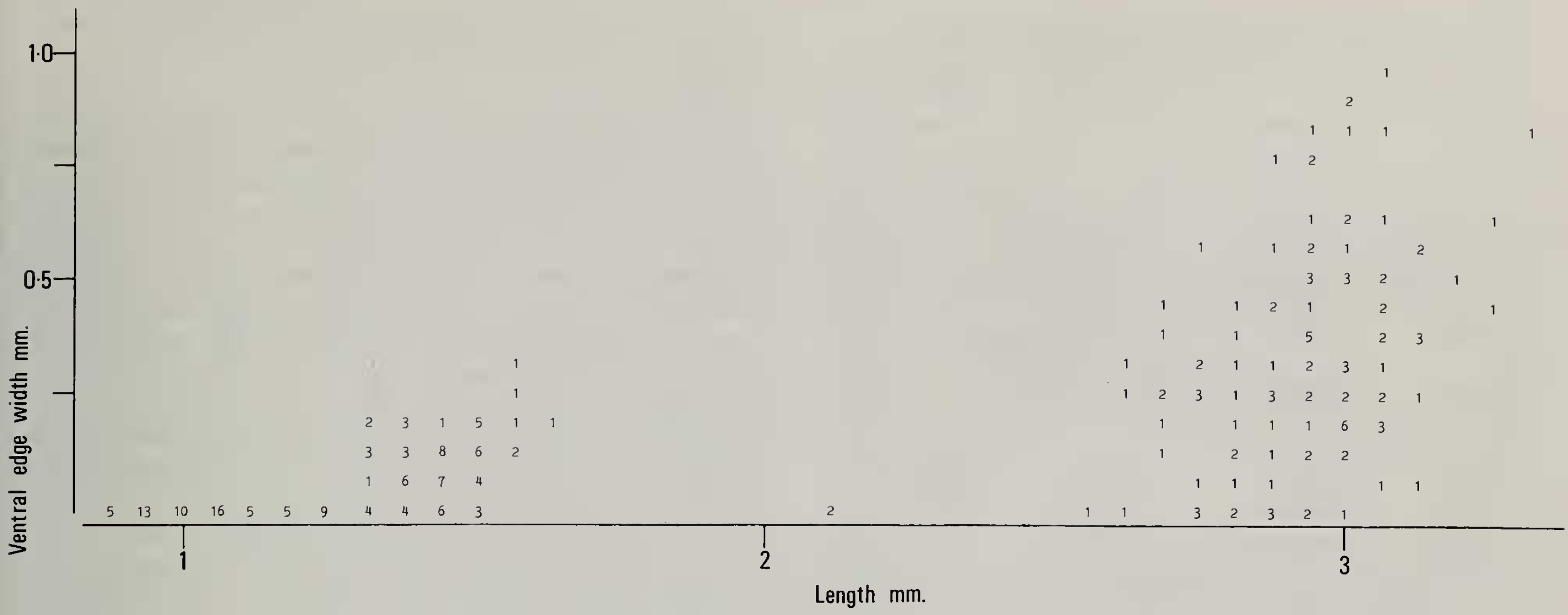

Fig. 70 *Ledella ultima*: An analysis of the width of the ventral shell margin plotted against length of specimens taken at Station 78.

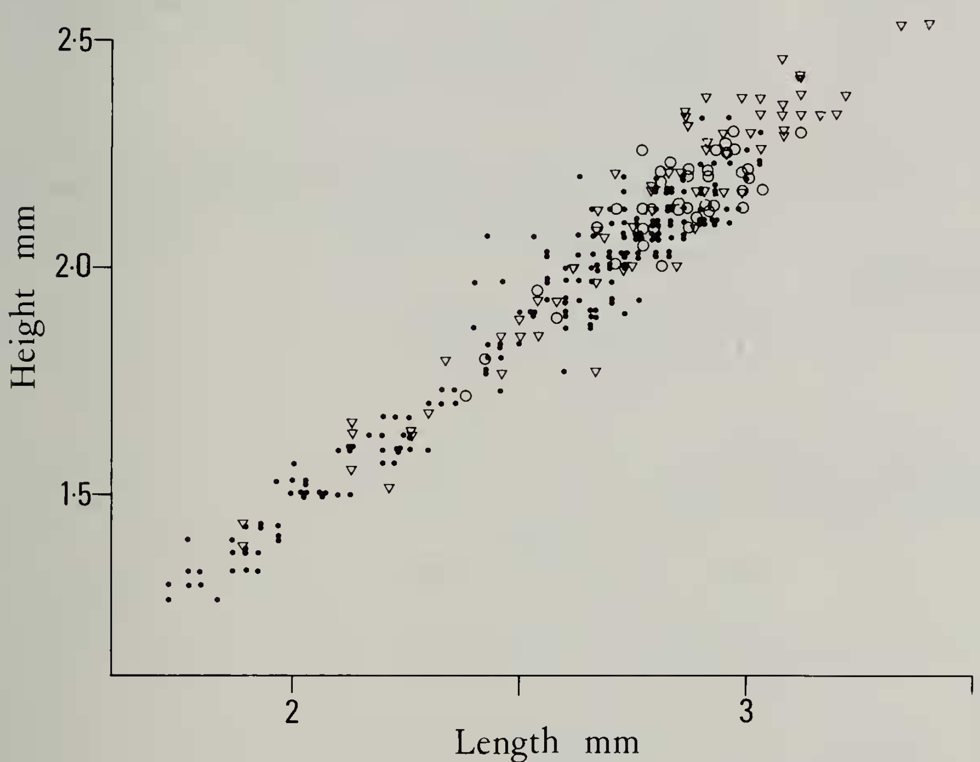

Fig. 71 *Ledella ultima*: The relationship between shell height and length compared for three Stations 148 (points) Walda DS31 (open circles) and Biogas VI DS84 (open triangles).

Basin), Sta. 148 (Cape Verde Basin), BGVI DS84 (W. European Basin), Sta. 101 (N. American Basin), Sta. 122 (N. American Basin) (Table 3).

Also, because of the very large numbers in the collections of this cosmopolitan species occurring over a wide band of abyssal depths it was possible to carry out a detailed statistical appraisal of the length, height and width relationships between and within populations. In short such differences as were found between populations were not statistically significant.

In this overall comparison the only difference between western and eastern Atlantic populations, and this is a visual one, is that North American specimens tend to have a less pointed rostrum with a more shallow ventral margin sinuosity, are slightly more rounded in outline, and the position of the umbo is slightly more variable but slightly more posterior on average. However, the variation within any sample is large (Fig. 74). No differences in internal morphology were observed.

Examination of the type specimens of *L. ultima, L. bushae* and *L. crassa* show some difference in the shape and thickness of the ornamental concentric ridges, but these differences are within the range of variation observed in any large sample of this species from any locality (Figs. 64, 73 & 74).

Despite the fact that a very small number of large eggs is produced by each individual, there seems to have been no evolution of population differences in the different abyssal basins let alone evolution of sibling species. Thus, the genus *Ledella* and *L. ultima* in particular, is in sharp contrast to the genus *Malletia* where varieties and sibling species are common (Sanders & Allen, 1982). This may be but a consequence of the commonness and continuum in the deep sea of *L. ultima*. There are clearly other possible explanations, the most likely being that in common with most other proto-

Table 2. Relationship between geographical distribution, depth of occurrence and hindgut morphology in species of *Ledella*

Species	Depth range (m)	Distribution	Rarity	Hind gut
L. p. hampsoni	2051–2357	Cape Verde	C	sl l & r
L. p. pustulosa	609–2659	S European–Canaries	C	sl l & r
L. p. marshalli	2496–4796	NW Scotland–SW Ireland	C	sl l & r
S. p. argentinae	3305–5223	Argentine	C	sl l & r
L. modesta	1661–4632	E European–Sierra Leone NE USA – Argentine	C	sl l & r
L. jamesi	1456–2853	Argentine – Guiana	C	sl l & r
L. lusitanensis	1624–1995	Biscay-Cape Verde	R	sl l & r
L. sandersi	1546–2154	SW Africa	MC/R	sl r
L. similis	1336	Biscay	R	sl r
S. verdiensis	3150–3155	Cape Verde	R	sl r
L. oxira	678–1493	SE USA-Argentine	R	sl r/l
L. galatheae	4279–4829	European-SW Africa	R	sl r/c
L. solidula	1000–1830	Surinam-Bermuda	MC	sl r/c
L. acuminata	475–1427	Bay of Biscay	MC	sl r/c
L. ultima	3196–5130	Cosmopolitan	C	c r
L. parva	450–960	E. USA	R	tl r & sl l

C = common; MC = moderately common; R = rare.
c = coil; l = left; r = right; r/c = loop on right passing to left close to anterior adductor then coiling; r/l = loop on right passing to left close to anterior adductor; sl = single loops; tl = two loops.

branchs, there has been little genetic change over many geological eras and over the entire geographic range of the species.

One of the notable aspects of size frequency histograms (Fig. 75) in all populations is the marked right hand skewness seen in all. In each case the maximum length observed is about 3.0 mm. This type of skewed histogram is typical of deep sea bivalves in which there are no large individual settlements of larvae. In shallow water species settlement followed by massive mortality results in histograms skewed to the left. In the case of *L. ultima* the right hand skew is compounded by the change in direction of shell growth. What initiates this change in growth is not clear, but it is tempting to postulate that this occurs after the release of the first batch of gametes. The advantage of small size to an abyssal benthic animal have been pointed out elsewhere (Allen 1978) yet it may be that this change gives advantage in that for no increase in lateral area of shell the volume of the mantle space is significantly increased. This allows for a marked increase in the number of eggs that can be accommodated and hence the breeding success of the species. It is also tempting to speculate that the greatly increased length of the hind gut accommodated by the tight coils, allows for increased assimilation of digested food and energy supply, which will also have reproductive advantage in this species.

Distribution. This is by far the most common and cosmopolitan protobranch species and is truely abyssal. N. American, Canary, Argentine, Angola and Agulhas Basins, Guinea Basin and Scotia Sea.

Depth range. 3196–5130 m.

Table 3. Comparison of shell dimensions in populations of *Ledella ultima*

Station	Max. Length mm	Max. VSM* mm	H/L Average**	H/L Range	W/L Average**	W/L Range	P.UL/TL Average**	P.UL/TL Range
WALDA DS31 (Guinea Basin) N=42	3.12	0.62	0.75±0.021	0.71–0.79	0.56±0.035	0.47–0.62	0.51±0.013	0.47–0.52
Stn. 122 (N. American B) N=106	3.10	0.82	0.76±0.026	0.71–0.84	0.50±0.035	0.41–0.60	0.48±0.030	0.40–0.55
Stn. 101 (N. American B) N=330	3.04	1.31	0.76±0.026	0.68–0.84	0.57±0.063	0.45–0.82	0.48±0.044	0.42–0.56
Stn. 148 (Cape Verde Basin) N=208	3.06	0.90	0.74±0.032	0.69–0.85	0.53±0.059	0.41–0.69	0.51±0.016	0.47–0.53
BGVI DS84 (W. European Basin) N=68	3.40	1.11	0.76±0.037	0.69–0.82	0.53±0.048	0.44–0.68	0.50±0.014	0.48–0.53

Note the slight difference between posterior umbonal length/total length between N. American samples and the rest. Umbos slightly more posterior in these than the others but they also have the greatest range.
** ± standard deviation.
* VSM – Maximum width of ventral shell margin.

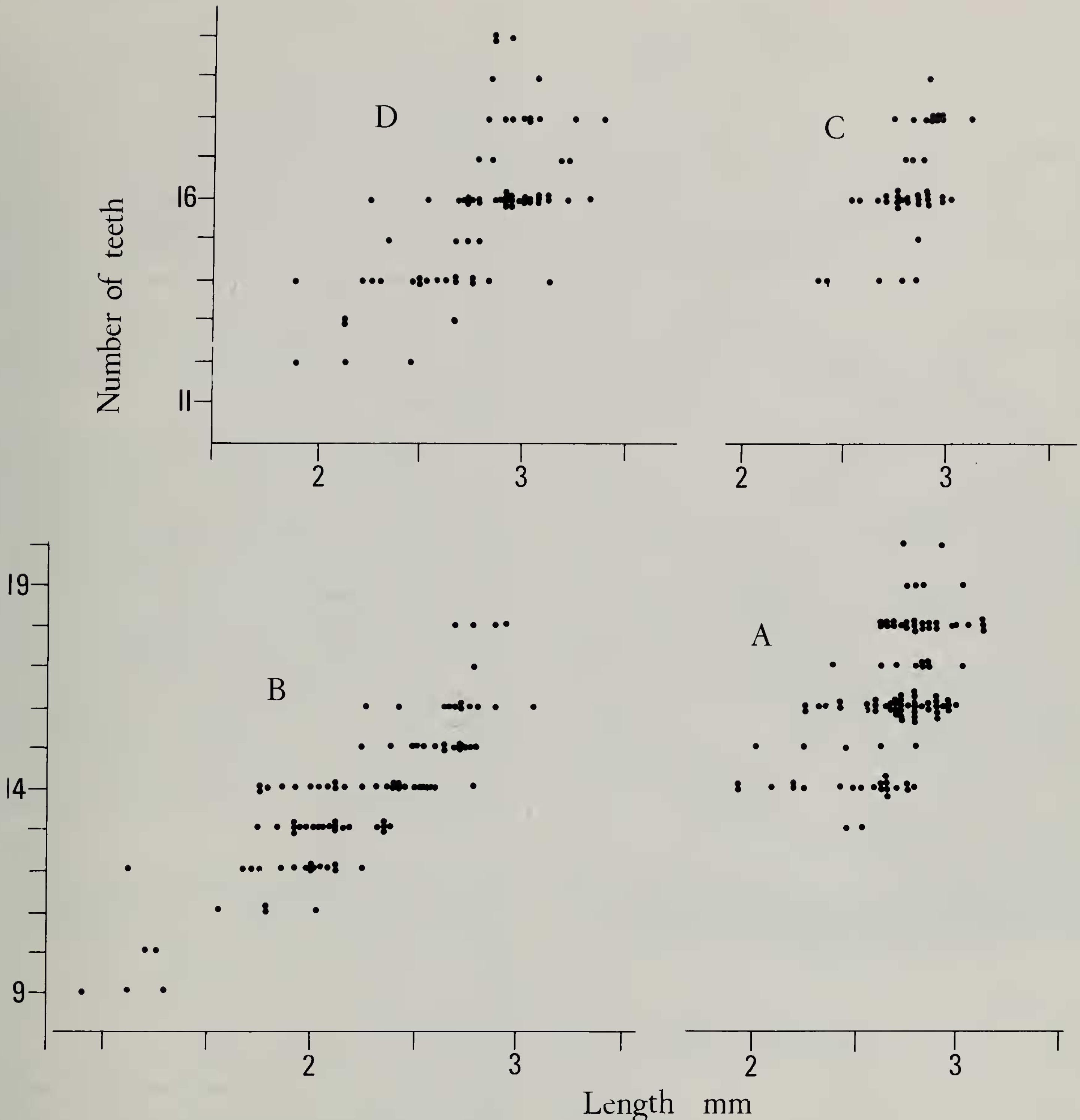

Fig. 72 *Ledella ultima*: The relationship between numbers of hinge teeth and shell length for four Stations a) 148; b) 122; c) Walda DS31 and d) Biogas VI DS84.

Ledella parva Verrill & Bush 1897

Holotype. U.S. National Museum (USNM) No. 78365.

Type locality. U.S. Fish Comm. Sta. 2689, off Martha's Vineyard, United States, 960 metres.

Synonymy. ?*Leda semen* Smith, 1885. *Rep. Lam. Chall. 13*, p. 231, pl. 19, Figs. 2 & 2a.
Ledella parva Verrill & Bush, 1897. *Am. J. Sci. 3*, p. 54, Fig. 18.
Ledella parva Verrill & Bush: Verrill & Bush, 1898. *Proc. U.S. natn. Mus. 20*, p. 857, pl. 81, Fig. 1.
Leda aspecta Dall 1927. *Proc. U.S. natn. Mus. 70*, art. 18, p. 9.
Nuculana semen (Smith): James, 1972. Ph.D. Thesis Texas A & M Univ. p. 119, Figs. 75 & 76.

Material.

Cruise	Sta.	Depth(m)	No.	Lat.	Long.	Gear	Date
USNM 78365	2689	960	?	Off Martha's Vineyard			?
Duke Univ. (Grassle)	349	450	2+ 2V	34°16.6'N	75°48.6'W	VV	7. 1.65
	3417	650	1	34°14.8'N	75°46.7'W	ES	29.11.65

Specimens of *Ledella semen* BM(NH) No. 1887.2.9 2925.
No. 1887.2.9. 2921–4.

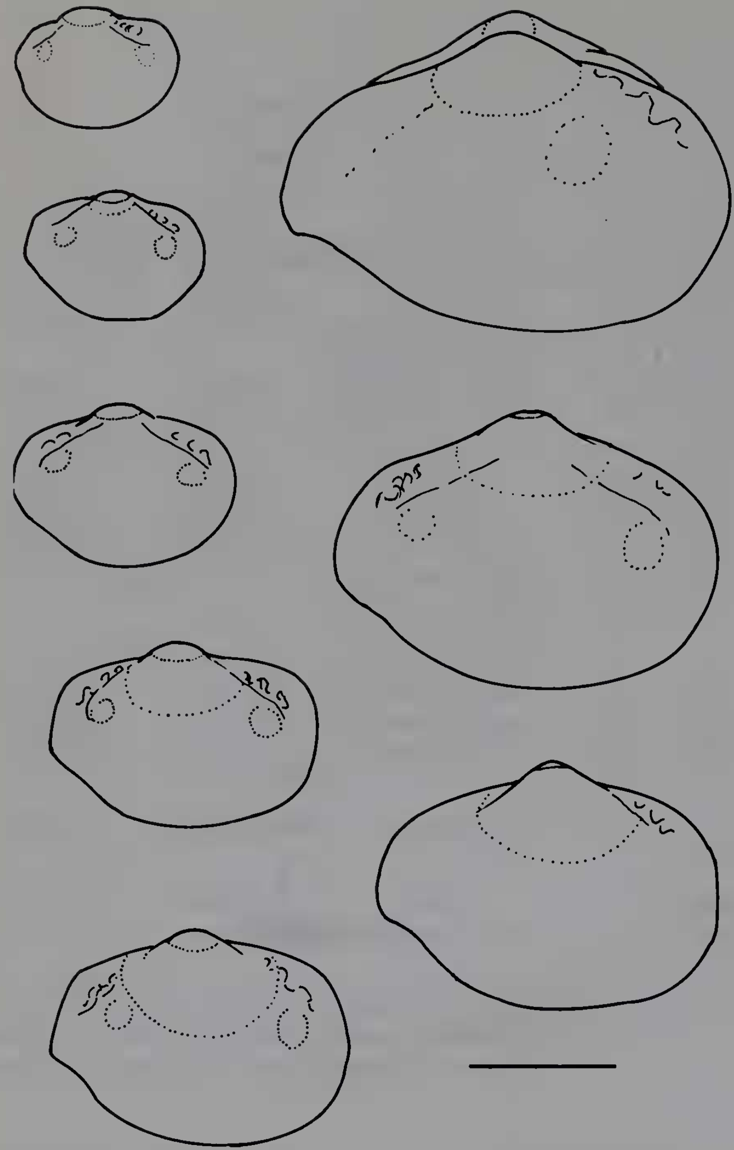

Fig. 73 *Ledella ultima*: Growth series of shells from Station 126 in lateral outline to show change in shape with increasing size. (Scale = 1 mm).

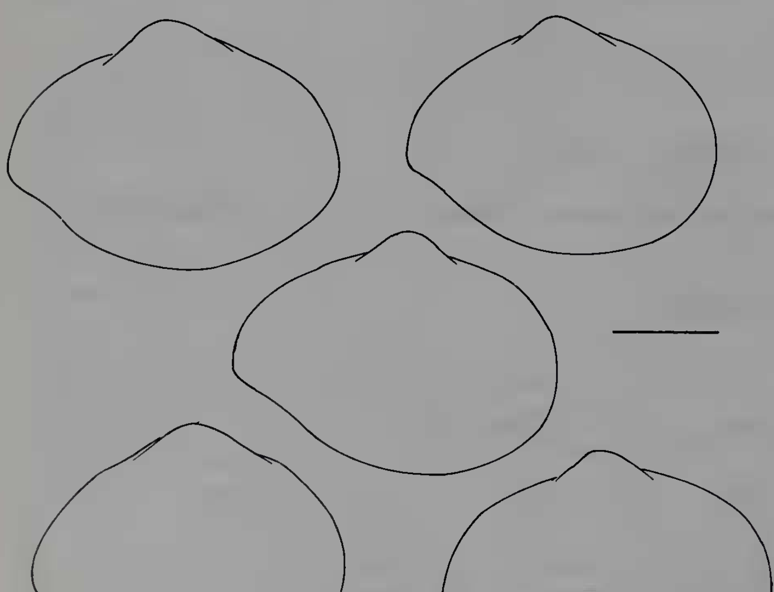

Fig. 74 *Ledella ultima*: Shapes of shells of similar length in lateral outline to show the range of variation within a single sample (Station 84). (Scale = 1 mm).

LOCALITY. Challenger St. 122, off Brazil, 9°05.'S, 34°51'W, 640 m.

Both specimens of *L. semen* labelled 'type' have disintegrated so that it is impossible to make comparisons with the type material of *L. parva* and with the present specimens.

From the descriptions of *L. semen* and *L. parva* and from what little can be made out of the fragments of the type species of *L. semen*, it is possible that *L. parva* and *L. semen* are synonymous. This conclusion was also reached by James (1978). James (1978) noted that Smith (1885) in his original description confused anterior for posterior teeth and *vice versa*. This we confirm. Verrill & Bush (1897) described *L. parva* as a separate species from *L. semen* on the basis of the teeth. Thus, while it may well be that the two species are synonymous, it would be unwise to be categorical. Note too that *L. parva* also resembles *L. oxira* (p. 148) and may be a sibling species.

DESCRIPTION (Figs. 76 & 77). Shell small, ovate, inequilateral, smooth, growth lines very fine; umbos posterior, slightly raised, slightly inclined posteriorly; anterior margin obtusely rounded, posterior margin with short rostrum, antero-dorsal margin curves from umbo in smooth curve with anterior margin, postero-dorsal margin proximally straight, more distally gradually slopes to a point opposite the posterior edge of hinge plate then more steeply to tip of rostrum, posterior ventral margin sinuous, ventral margin rounded, moderately convex, shallow depression in shell from umbo to postero-ventral margin; hinge plate moderately strong, broad, posterior hinge plate short, strongly curved with 9 chevron-shaped teeth, anterior plate less curved with 12 teeth; ligament amphidetic, internal, triangular in shape.

The dimensions of the two intact specimens from Station 349 are as follows:-

Length(mm)	Height(mm)	Width(mm)	H/L	W/L	P.umbo/Total	Teeth Ant/Post
2.6	1.72	valv. sep.	0.66	–	0.40	12/19
1.12	0.84	0.52	0.75	0.46	0.42	–

MORPHOLOGY. Only three specimens were available for study and this description has been based on a single whole mount (Fig. 78).

The mantle structures differ little from those described for the other *Ledella* species. The combined siphon is moderately muscular and elongate, the siphonal tentacle is inserted at the base of the siphon on the left side. The anterior sense organ is anterior to the anterior limit of the anterior adductor muscle. The adductor muscles are large, the posterior muscle is approximately circular in shape while the anterior muscle is larger (1.5x) and bean-shaped in outline.

The foot is large and anteriorly directed. The 'byssal' gland is large. The gills lie deep within the mantle cavity (Fig. 78) but this may be a distortion due to the retracted siphon. Approximately 15 alternating gill filaments are present. The palps are moderately small with 9 ridges and the palp proboscides are elongate and slender. The mouth is situated a short distance behind the anterior adductor muscle and opens into a wide oesophagus to a large stomach. A small style sac penetrates a short distance into the foot. The hind gut penetrates level with the pedal ganglia and then turns 180° passing posterior to the stomach, to the dorsal margin of the

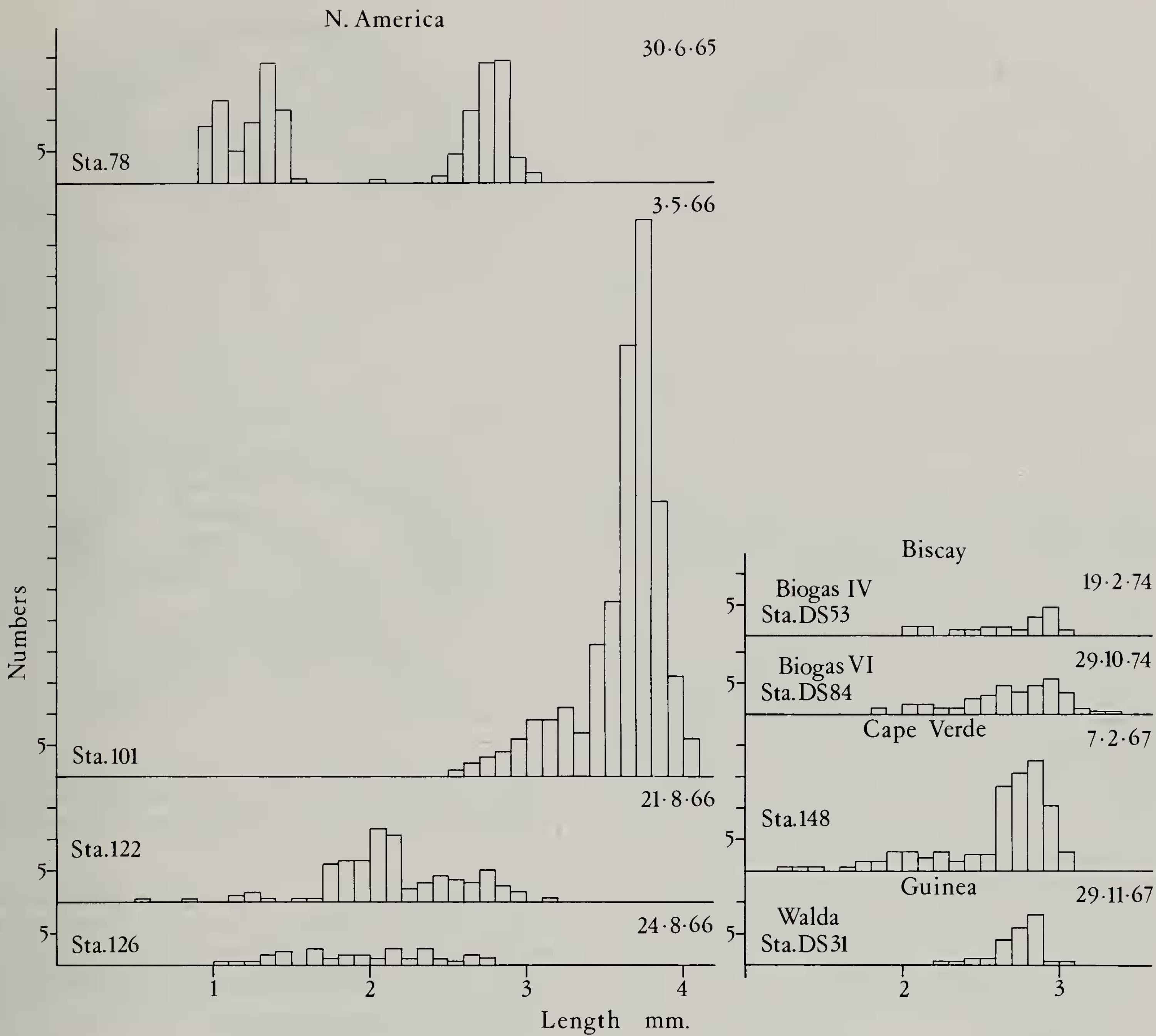

Fig. 75 *Ledella ultima*: Size frequency histograms for samples from eight Stations.

body to form a loop on the right side of the body. Its course takes it close to the anterior adductor muscle and then to a point immediately posterior to the ligament where it crosses to the left side of the body to describe a similar loop to that on the right. Thereafter it passes to the right side for a second time, immediately posterior to the first cross over point, and makes a second loop on the right close to, and in parts superimposed on, the first (Fig. 78). The dorsal section of this second loop passes to the anus posterior to the posterior adductor muscle.

The pedal ganglia are large and situated in the neck of the foot. The visceral and cerebral ganglia are typically cylindrical in shape; the visceral ganglia terminate close to the posterior adductor muscle.

Distribution. Upper continental slope off East coast of United States, Gulf of Mexico.

Depth range. 450–1180 m.

Ledella sp.

Material.

Cruise	Sta	Depth(m)	No.	Lat.	Long.	Gear	Date
		NORTH ATLANTIC BASIN					
Chain 50	83	5000	1	34°46.5′N	66°30.0′W	ES	3. 7.65
Atlantis II 24	121	4800	1	35°50.0′N	65°11.0′W	ES	21. 8.66
Atlantis II 13	123	3853	1	37°29.0′N	64°14.0′W	ES	22. 8.66

Only three specimens were taken from abyssal depths from the North Atlantic Basin, one of which was an intact dead shell. No whole preparation has been made. As a result we do not wish to define a new species, although we believe that when further specimens are obtained it may well prove to be so. Here we simply record a shell description.

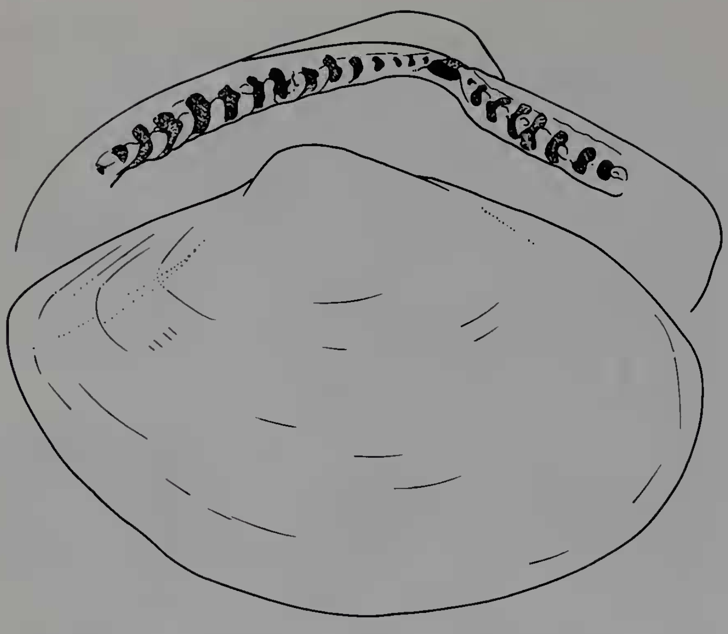

Fig. 76 *Ledella parva*: Right lateral external view of the type specimen (USNM No. 78365); and internal view of hinge region of right valve of the same specimen. (Scale = 1 mm).

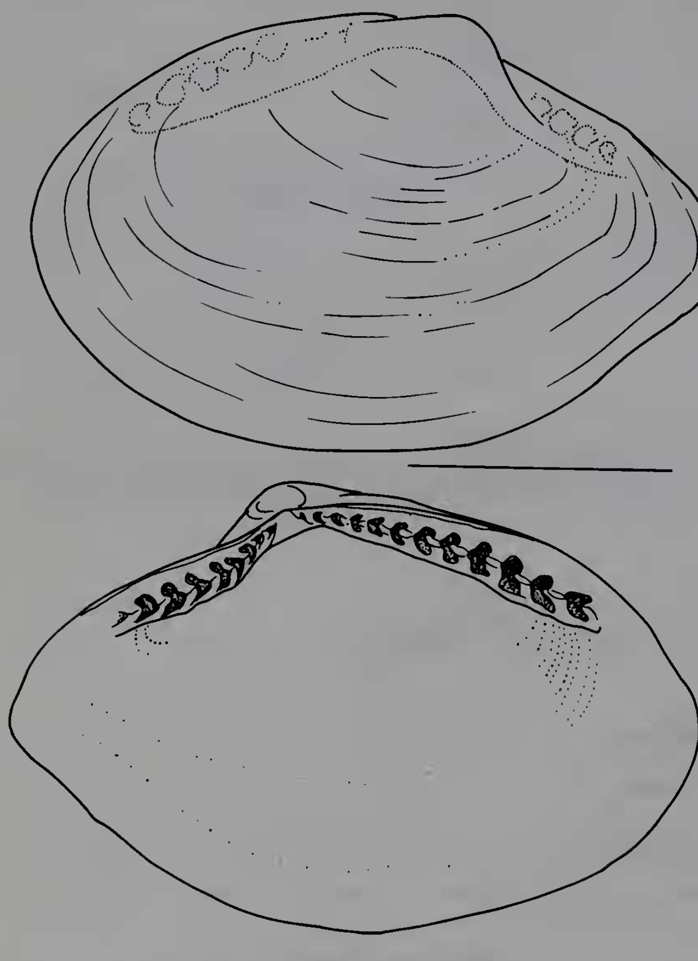

Fig. 77 *Ledella parva*: Left lateral external view of specimen from Duke University Station 349 and internal view of left valve of same specimen to show hinge detail. (Scale = 1 mm).

DESCRIPTION (Fig. 79). Shell robust, ovate, inequilateral, rostrum relatively short, concentric ridges; umbos moderately large, posterior to mid line, directed medially; antero-dorsal margin slopes moderately sharply to curve continuously with narrow anterior margin, postero-dorsal margin slopes moderately sharply to posterior limit of hinge plate to form angle with dorsal margin of rostrum, postero-ventral margin broadly sinuous giving characteristic undercut appearance to shell,

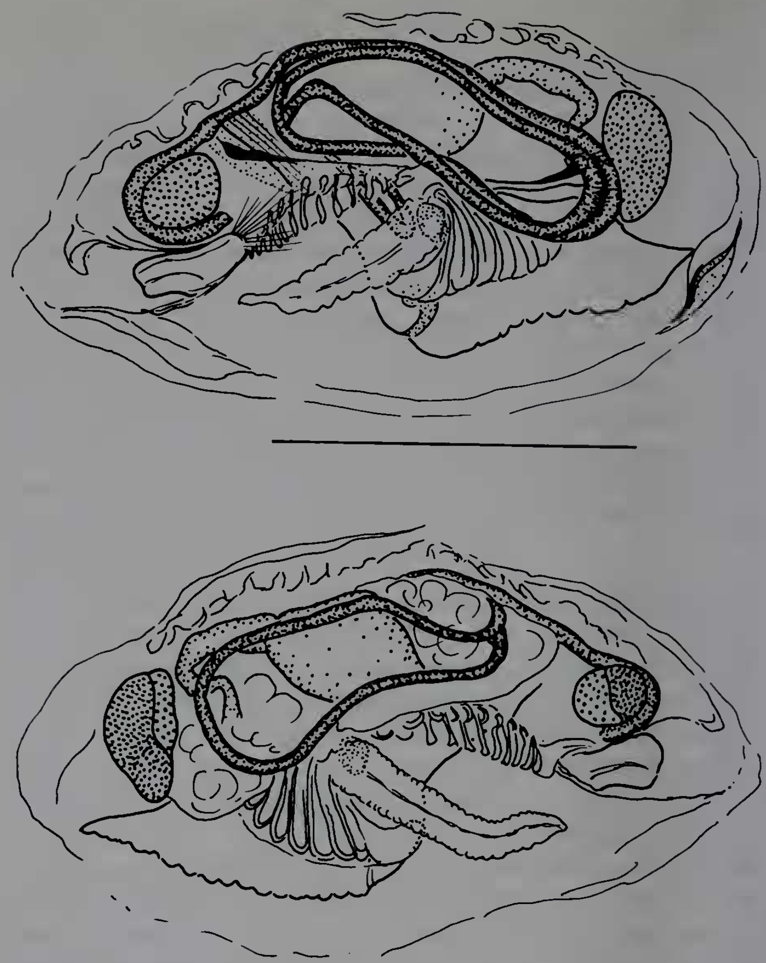

Fig. 78 *Ledella parva*: Lateral view of a specimen from the left and right sides with the shell removed to show the arrangement of the body organs (Station 349). For identification of parts see Fig. 42. (Scale = 1 mm).

rostral ridge moderately strong; hinge plate elongate, fairly broad along entire length, hinge teeth short, broad chevrons except for 3 proximal teeth of anterior and posterior series ventral to umbos; resilifer broad trapezoidal; ligament amphidetic, internal.

Maximum shell length: 5.2 mm.

DISTRIBUTION PATTERNS

Species of *Ledella* do not occur on the continental shelf. Analysis of the fourteen species described here (Fig. 80, Table 4) shows that most are restricted to the slope and abyssal rise. Many are rare species restricted in their horizontal distribution, for example, *Ledella parva, L. similis* and *L. sandersi* are restricted to the East coast of the USA, Biscay and South West Africa respectively. Others including *L. oxira, L. lusitanensis, L. solidula* and *L. acuminata*, which are a little less rare, spread further along slope, but with either no or relatively little geographical overlap. Rare species also occur at abyssal depths, of these one is the as yet unnamed *Ledella* from the North America Basin, the other *L. verdiensis* is from the Cape Verde Basin.

Of those that remain *L. ultima*, is the most common protobranch in the Atlantic. Except for the Norwegian Basin it occurs throughout the ocean at abyssal depths. The common widespread counterpart at slope and lower abyssal rise

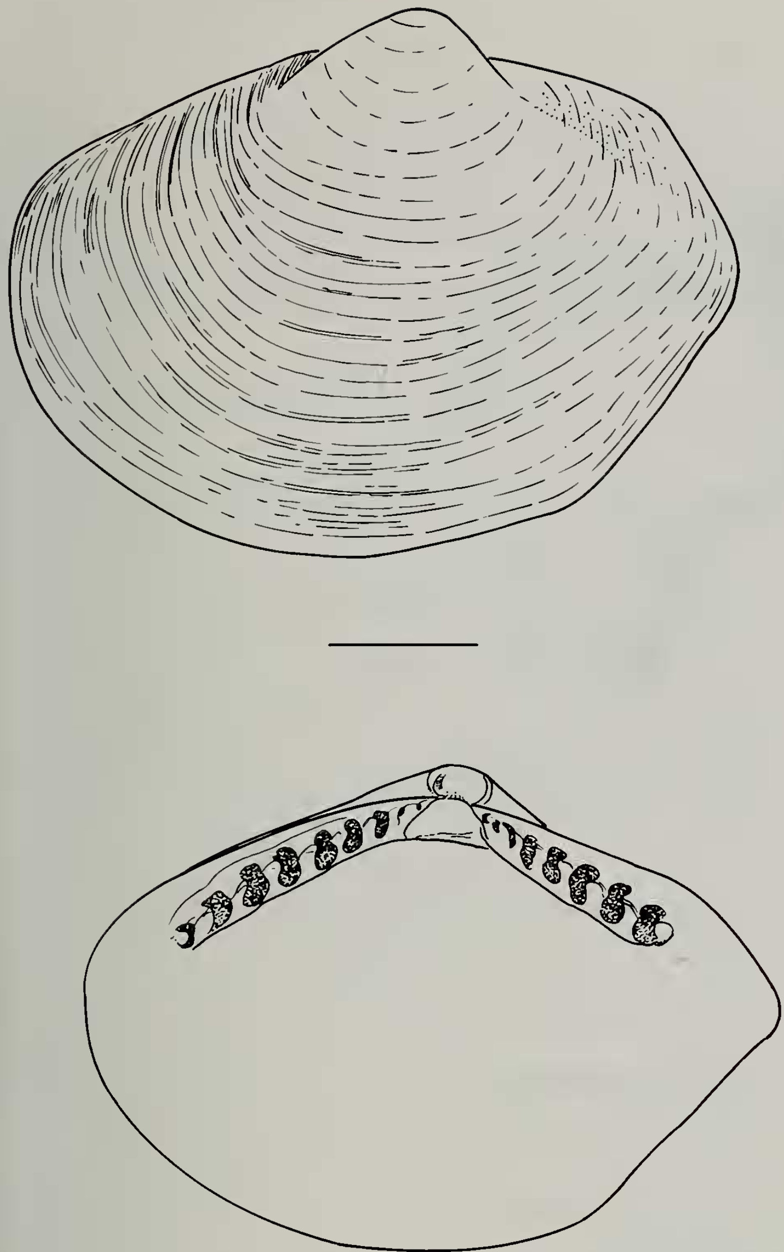

Fig. 79 *Ledella sp.*: Left lateral external view of shell of the specimen from Station 123 and lateral internal view of right valve of specimen from Station 83 to show hinge detail. (Scale = 1 mm).

depths is the *L. pustulosa* complex. This latter species appears to be in the process of speciation and here we recognise four closely related subspecies. Two, *L. p. pustulosa* and *L. p. marshalli*, while overlapping latitudinally in the North East Atlantic, are allopatric occurring on the slope abyssal rise and the upper abyssal depths respectively, the other subspecies, *L. p. argentina* and *L. p. hampsoni*, are geographically separate at abyssal rise depths. *L. modesta*, another common and widespread species, occurs somewhat deeper than the *L. pustulosa* complex. From these examples it is possible to make some general conclusions about the distribution of *Ledella* in the Atlantic and, from experience, also apply generally to the protobranch bivalves of the deep sea.

1) that common truely abyssal species are widespread in their occurrence.
2) common species of the slope and abyssal rise show sufficiently discernable population differences in shell form to an extent that true subspecies may be recognized.
3) rare species of the slope appear to have restricted distributions.

Occasional exceptions can be found to these general rules. Thus, *L. jamesi* common in the Argentine and Guinea Basins does not occur to the north and to the east. Such a distribution is known from other protobranch groups (Allen & Sanders in m/s, Sanders & Allen, 1965). In addition the benthic slope and abyssal bivalve faunas of the Argentine and Guiana Basins tend to have a high degree of endemism, but, unlike the impoverished fauna of Norwegian basin which also has a high degree of endemism, the isolated fauna off the East coast of South America is relatively rich in species. This is possibly correlated in some way to the north moving, relatively organically rich bottom water.

MORPHOLOGICAL EVOLUTION

Comparison of the specific morphologies of shells and various body organs shows that in common with most deep sea protobranch genera, the shell of *Ledella* is conservative in form with little variation in outline and sculpture. Similarly, with the exception of the configuration of the hind gut, there is little variation in the morphology of the viscera and such as there is, eg. adductor muscle size, can usually be related to other parameters such as the strength of the hinge and the size of the ligament.

The configuration of the hind gut in *Ledella* has considerable evolutionary significance. The various species of *Ledella* exhibit all the major hind gut configurations that are present in nuculanoid protobranch bivalves in general. The configurations are a consequence of the lengthening of the hind gut and the need to accommodate it in limited body space in the most advantageous way. The primitive nuculanoid condition is a single loop to the right side of the body. This is seen in three of the rarer species, namely *L. sandersi, L. similis* and *L. verdiensis*. All are from the East Atlantic at mid slope or abyssal rise depths. Modification of this configuration appears to take two forms. In one the loop of the gut extends to the left side of the body via the space between mouth and the posterior face of the anterior adductor muscle. On the left it may (*L. galathea, L. solidula, L. acuminata*), or may not (*L. oxira*), coil upon itself. In the other form, there is a loop *first to the left* and then to the right side of the body crossing to each side posterior to the stomach. (*L. pustulosa, L. modesta, L. jamesi* and *L. lusitaniensis*). Species exhibiting these two main types of configuration are found throughout the Atlantic from upper slope to abyssal depths. Finally, there are two species which have other configurations. In the case of *L. ultima* the hind gut has multiple coils on the right side of the body. This, like loop extended to the left and there coiling, is easily derived from the primitive condition by coiling the single loop several times (Fig. 81). This configuration is also typical of many species of *Spinula* (Allen & Sanders 1982) and seems to be particularly associated with those species living at abyssal depths. It is a device that simply ensures the maximum extension of the gut within a limited volume of body space. One further condition, to date found only in *L. parva*, is two loops to the right and one to the left. This too can be derived from the primitive condition, the first loop to the right being the proximal part of the hind gut. *L. parva* has a restricted distribution on the upper slope of the East coast of the United States and, for an upper slope species it has an extremely long gut.

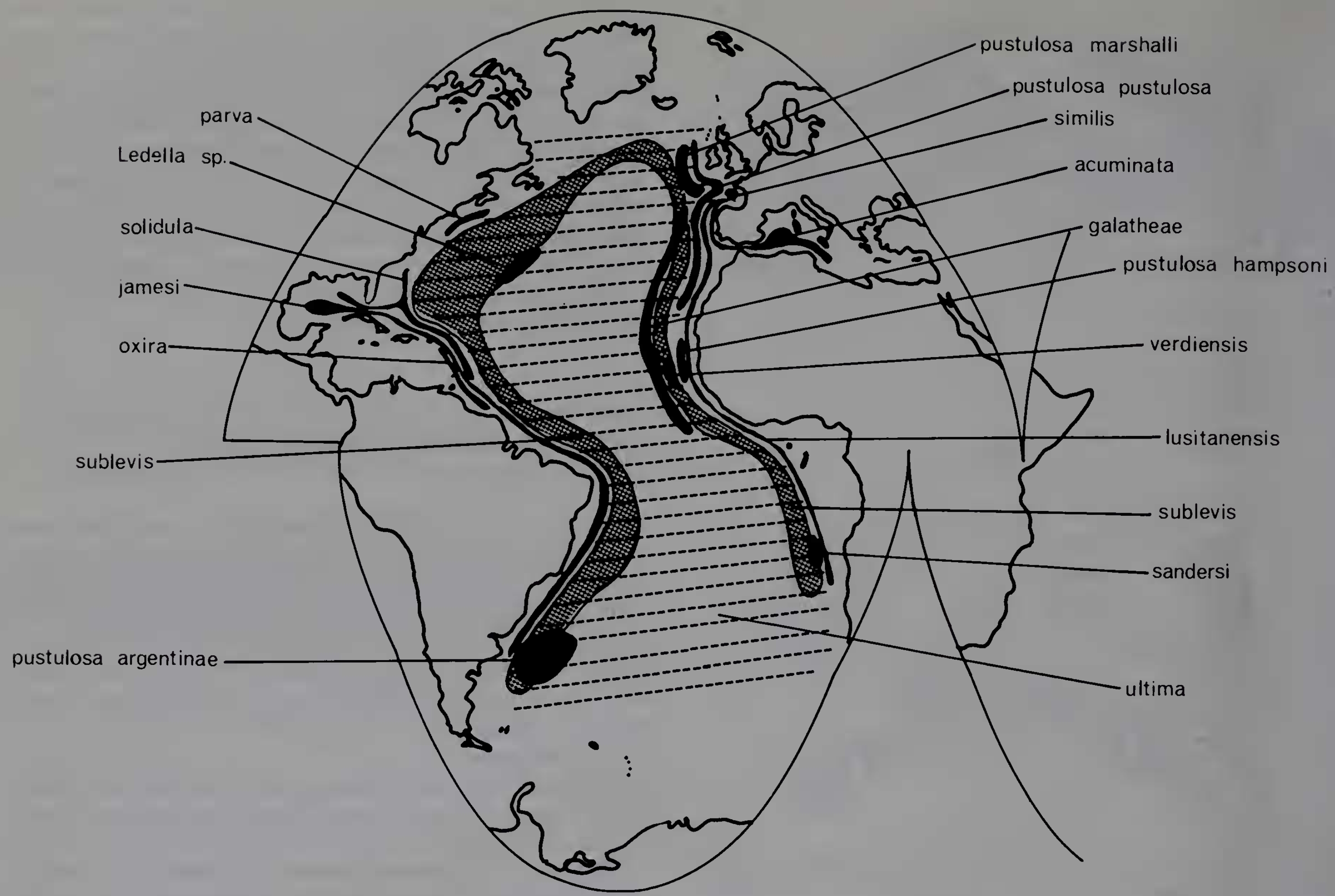

Fig. 80 The distribution of the *Ledella* species in the Atlantic.

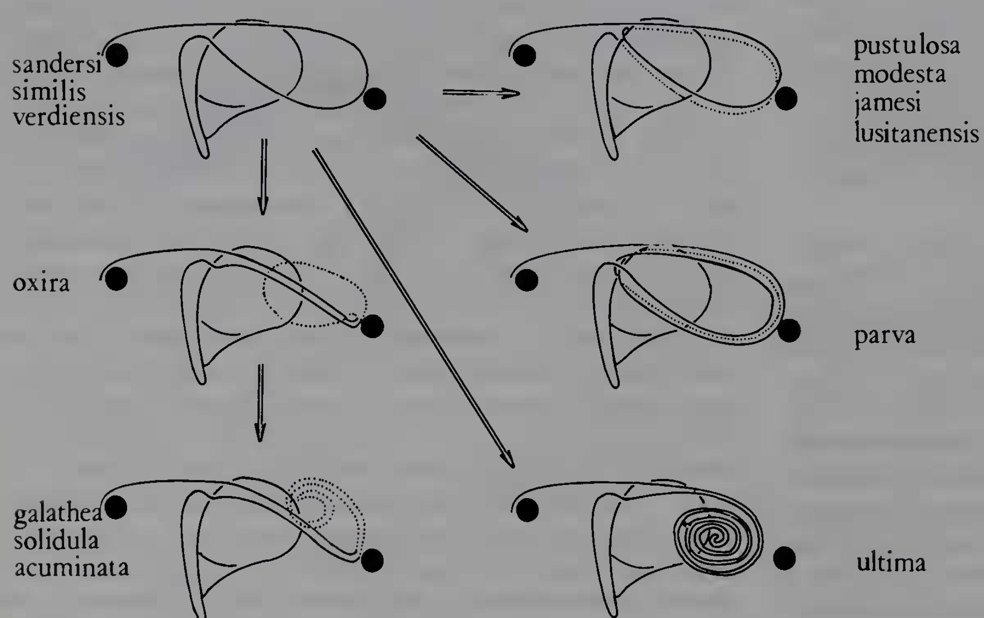

Fig. 81 The radiative evolution of hind gut configurations in species of *Ledella*.

Thus, the length of the hind gut and its relationship to the depth at which its possessor lives is not entirely consistent. Species possessing a short single loop are not all found at slope depths, but in general most abyssal species have long hind guts. Conversely elongate hind guts can be found in a few upper slope species and presumably give digestive advantage.

In a small species an enlarged gut has the disadvantage of restricting the space for gonadial development but then food reserves are in such short supply in deep water as to limit egg production. Presumably there is a fine balance between energy supply and space apportionment. In this regard adaptive advantage would appear to be in the exceptional change of direction of shell growth as seen in *L. ultima* and with the consequent enlargement of shell space. *L. ultima* is certainly the numerically and geographically the most successful species of the subfamily.

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